5-2018

Water-Electricity Nexus: Assessing Impacts of Habitat Loss on Freshwater Mussel Assemblages in the Savannah Basin, South Carolina

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WATER-ELECTRICITY NEXUS: ASSESSING IMPACTS OF HABITAT LOSS ON FRESHWATER MUSSEL ASSEMBLAGES IN THE SAVANNAH BASIN, SOUTH CAROLINA

A Dissertation
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Wildlife and Fisheries Biology

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by
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May 2018

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ABSTRACT

The environmental effects of energy production are well known, yet its exact impacts on freshwater resources are often difficult to recognize and measure. Freshwater mussels are extremely imperiled organisms which act as sentinels of freshwater streams and are greatly understudied in context of their drastic decline caused in part due to large water demands by the energy sector. I sought to estimate historic, current and forecasted water use by electricity generation at national, regional and local- scale. To relate the impacts of water-use by electricity generation on freshwater mussels, I conducted occupancy surveys for eight freshwater mussel species in Savannah River Basin, South Carolina. I modeled landscape and local factors potentially influencing occupancy and assessed whether the occupancy of species indicated vulnerability to the presence of impoundments. I also modeled the viability of the endangered Carolina heelsplitter (*Lasmigona decorata*) metapopulation in response to habitat loss caused by water appropriation associated with the energy sector. The results suggest that water-use is projected to increase in the future irrespective of clean energy policies and variety of energy mix. The water consumption is predicted to increase at a local scale and the water withdrawals will vary spatially and temporally. The site occupancy varied with species and was significantly correlated with local habitat factors such as stream width and substrate heterogeneity and landscape driven factors such as % forest and presence of impoundment. The Carolina heelsplitter metapopulation exhibited a gradual decline in response to both habitat degradation and fragmentation for both effective population sizes, but the effect was more significant at lower population sizes. The findings of this

dissertation suggest that mussel assemblages in the Savannah river basin are more likely to benefit from habitat restoration than the removal of dispersal barriers and management efforts for threatened mussel species should prioritize habitat protection and restoration.

DEDICATION

This work is dedicated to the loving memory of my grand-uncle, Mr. Janardhan Patil for his continual support and encouragement towards the pursuit of higher education. Thank you, Mama Ajoba, through your legacy you'll be constant source of inspiration and motivation.

ACKNOWLEDGEMENTS

I would like to express my gratitude to many people who contributed and helped in the completion of this dissertation. First and foremost, I thank my academic advisor and guide Dr. Alan Johnson for his constant support, unfailing encouragement and useful critiques during my tenure as a doctoral student. You provided me with a valuable opportunity of selecting a research subject of my own choosing and for that I am extremely grateful.

I would like to thank my advisory committee, Dr. Kyle Barrett, Dr. John Rodgers and Dr. Johns Hains for their time, insight and much appreciated guidance in conceptualizing and implementing this research project. I would like to thank Dr. William Bridges for providing valuable statistical expertise. I would like to extend my gratitude to the Clemson University's Department of Biological Sciences (College of Science) and Department of Forestry and Environmental Conservation (College of Agriculture, Forestry and Life Sciences) for supporting me financially with graduate teaching and grading assistantships as well as the Graduate Student Government's Professional Enrichment Grants for travel support.

Chapters 2, 3 and 4 of this dissertation are publications proposed for submission to peer-reviewed journals. Chapters 2 and 4 are co-authored with Dr. Alan Johnson and Chapter 3 with Dr. Kyle Barrett and Dr. Alan Johnson. I appreciate the contribution of the principal collaborators towards project design, statistical analysis of data and reviewing of manuscripts. I extend my gratitude to Morgan Wolf of United States Fish and Wildlife Service for her help in identifying freshwater mussel species and in data collection. Morgan, you were always patient and understanding and a great mentor. Thanks for accompanying me on the long field visits and spending the hot summer days half submerged in water looking for the spectacular Carolina Heelsplitter. Shefali Azad- Thank you for your help with the data collection. I am glad to have known you in the capacity of a colleague and friend.

My friends in India and United States- thanks for your support, love and words of wisdom. A few names warrant special thanks. Sneha- you have always believed in me and encouraged me to follow my dreams. Neela for being my first friend at Clemson and an unfailing guide. Neel, Dani and Arun for being your awesome selves and for lending an eager ear whenever I felt like venting out. Sukh for being a terrific roommate and an even better friend/soul-sister. Hrishi for your advice when I needed it the most and being able to share my love for books with you. Kanika, our shared fondness of Harry Potter and pop-culture kept me cheerful even during the gloomiest times. Sriram, Venky, Preethi, Clara, Krithika and Navdeep thanks for being solid friends and I am thrilled to have you all in my life. My old office mates; Cady, Carly and Karen- thanks for making me feel welcome at Clemson and in the department; and the recent ones, Caroline, Juliet and Yvan- for being such motivating colleagues.

My family- I am grateful for your support through all the highs and lows. My godparents- Drs. Rita and Rajeev Dhamankar, your constant inspiration and valuable advice mean a lot to me. My parents, Drs. Pratibha and Subhash Mhatre - I am eternally indebted to you for inculcating the values of kindness and compassion, for stimulating intellectual curiosity since a young age, and for the endless words of encouragement every time I wavered. Shruti, you are a fantastic sister and a delightful ray of sunshine in my life. Lastly, Utkarsh Patil- my friend since the beginning, fiancé for the middle part and husband now. Thank you for your refreshing comedic interjections and for your firm belief and unfaltering faith in me all along. Without your constant love and support none of this would indeed be possible.

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CHAPTER ONE

INTRODUCTION

The International Energy Agency states that no energy source, renewable or non-renewable exists without risk and that each comes associated with a certain environmental, social, economic or technological disadvantage (International Energy Agency (IEA), 2012). The world and regional energy scenes are in constant flux, and hence when it comes to choosing energy sources many aspects must be considered. Energy and water are the world's two most interdependent resources and equally important for social equity, ecosystem integrity and economic sustainability (WBCSD, 2009). We use energy to process surface and ground water making it potable, for supply and transmission of water and for treating industrial and municipal wastewater. On the other hand, we use water to produce energy for industry, electricity and transportation. All forms of energy production, energy distribution, fuel extraction, and fuel refinement utilize water in one way or other (Figure 1-1)

Fresh water makes up a very small fraction of all water on the planet and has several competing uses in energy extraction and production, agriculture, industrial/municipal use and drinking water supply. The inefficient use of the water resources in several parts of the world has caused severe water shortages which are only worsened by the impact of climate change. Globally, energy is the second highest withdrawer of water following irrigation. The energy sector is expanding due to increasing population and rising economic growth and will continue to exert pressure on fresh water demand in many river basins and countries (Figure 1-2). Climate change is intensifying the water-stress induced by energy demands by changing the hydrological cycle and causing uncertain shifts in seasons leading to higher temperatures and drier summer months in some regions of the world and wetter winter months in other parts (Barczak & Carroll, 2007; International Energy Agency (IEA), 2015; Zhang & Anadon, 2013).

Production of energy from any primary source has detrimental ecological consequences and the impacts vary spatially depending on whether the nexus exists in a water-scare or water-rich region. Excessive water appropriation during energy production severely compromises the biological integrity of the aquatic ecosystems in the form of habitat loss (Bain, 2007; Newton, Woolnough, & Strayer, 2008; Richter, Mathews, Harrison, & Wigington, 2003)**.** Maintaining environmental flows is critical to ensuring river systems can supply water for economic development and ecosystems. The trade-off between water security for energy and environmental conservation will become more complex under a water-constrained future along with the challenge of climate changed-induced extended periods of aridity, (Allen, Galbraith, Vaughn, & Spooner, 2013; Barczak & Carroll, 2007). However, there remains a lack of understanding in the precise effects of energy sector's water demands on aquatic systems and the organisms such as fish and freshwater mussels that inhabit them**.**

The IUCN estimates 126,000 species rely on freshwater habitats of which 45% are fishes and 25% are freshwater molluscs. Freshwater biodiversity is facing unprecedented levels of decline due to anthropogenic disturbances such as electricity generation, water storage, altered water quality and quantity, water pollution, siltation, habitat loss and habitat degradation, with some taxa and groups being more severely threatened than others. (Dudgeon et al., 2006; Naiman & Turner, 2000; Richter, Braun, Mendelson, & Master, 1997; Vaughn, 2010). As we continue to manipulate aquatic resources the risk of decline of aquatic organisms is bound to increase, which in turn disrupts the ecosystem services performed by these aquatic bodies (Kennedy and Turner, 2011).

Presently, 48.5% of freshwater mussels, 23% of freshwater gastropods, 33% of crayfish, 26% of amphibians and 21.3 % of freshwater fishes are critically imperiled (Ricciardi & Rasmussen, 1999). Freshwater mussels (Family Unionidae) are the most endangered of all organisms in North America (Haag, 2012a; D. L. Strayer, 2008; Williams, Warren Jr, Cummings, Harris, & Neves, 1993). They are widely distributed in North America with 297 recognized taxa of which only 70 are considered to be stable (Williams et al., 1993). Freshwater mussels play important role in the function and maintenance of healthy freshwater ecosystems (Haag & Williams, 2013; Lydeard et al., 2004) and are widely recognized as multifaceted indicators of ecosystem health (Grabarkiewicz & Davis, 2008). They can prove to be useful models to study the diffuse and chronic impacts of habitat degradation and fragmentation as they are sedentary, long lived (Bauer & Wächtler, 2012) with a reproductive cycle (Figure 1-3) requiring specific fish host species (Strayer et al., 2004), sensitive to water pollution (Cope et al., 2008), and hence susceptible to extinction debt (Strayer et al., 2004; Vaughn, 2012). Though several conservation and restoration efforts have been carried out to slow the mussel population decline, much of the information needed to identify and remedy the threats is difficult to find. The available literature on mussel decline is anecdotal at best. However, majority of the publications on freshwater mussels, identify pollution, flow alteration and habitat degradation and fragmentation as the most likely causes of decline (Strayer et al., 2004).

The Southeast United States is a mussel biodiversity hotspot with more endemic freshwater mussel species than any other region in the world (R. J. Neves, Bogan, Williams, Ahlstedt, & Hartfield, 1997; Peterson, Wisniewski, Shea, & Jackson, 2011a). This region also experiences high demands of water for energy production severely affecting the availability of freshwater (USDOE, Dec 2006) leading to several watersheds already running out of water to utilize. Given continued growth and subsequent industrial, agricultural and metropolitan demand throughout the southeast, the threat of water related conflict is imminent with the probability of intensifying in the future.

This research project seeks to quantify the electricity-water nexus and its environmental impact on aquatic biota, specifically freshwater mussels (Figure 1-4). Chapter 2 of this dissertation focuses on disentangling the electricity-water nexus, by estimating the water withdrawn and consumed by electricity generation by different energy sources and exploring the spatial and temporal trends associated with water use by electricity production. Chapter 3 seeks establish influence of local and landscape factors on the distribution and abundance of freshwater mussels in the affected stream networks in Savannah river basin by employing the occupancy modeling approach. Chapter 4 uses a combination of metapopulation and population viability modeling approach to evaluate impacts of hydrologic alterations in form of habitat loss by assessing the extinction risk of the endangered Carolina heelsplitter (*Lasmigona decorata*) in the Turkey creek watershed, Savannah Basin, SC. Chapter 5 offers a compilation of the key conclusions and provides recommendations for conservation and management of freshwater mussels in the Savannah River Basin in South Carolina.

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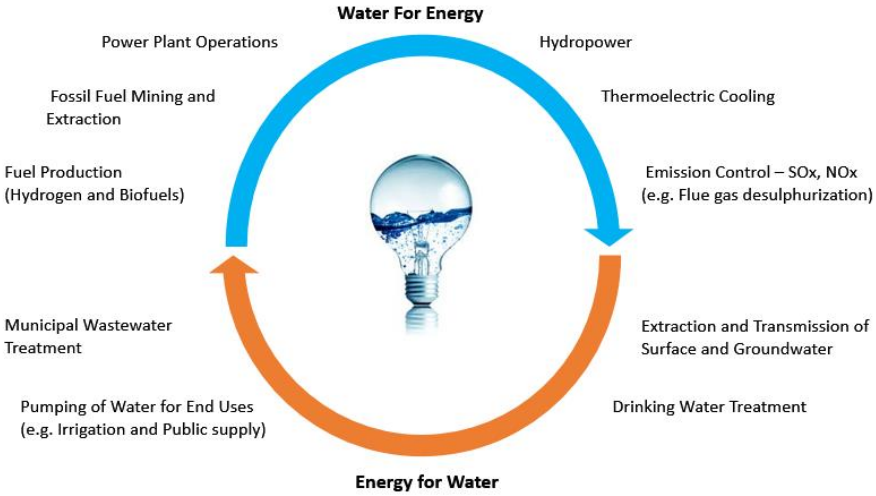
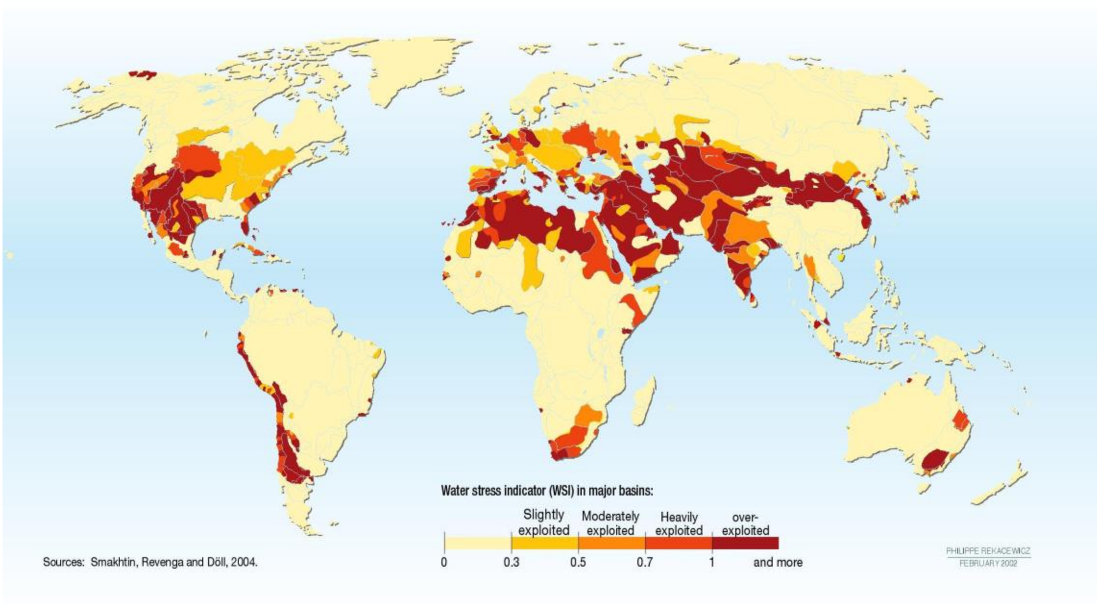
Figure 1-1: Pictorial representation of the Water-Energy Nexus[2,3].



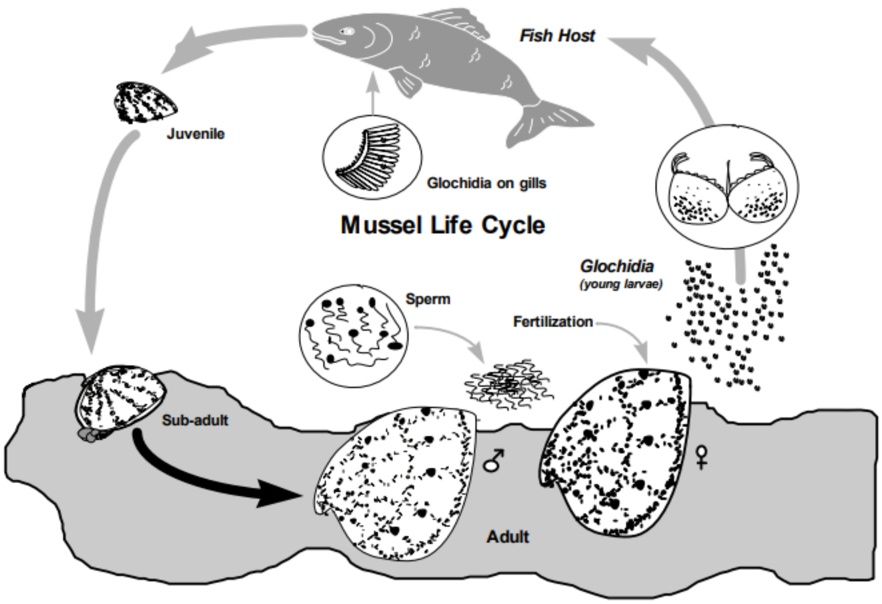
[2] Modified and Adapted from: WBCSD. (2009). *Water, energy and climate change: A contribution from the business community*. Conches-Geneva, Switzerland: World Business Council for Sustainable Development.
[3] Image downloaded from http://pacinst.org/issues/water-energy-nexus/ in September 2017 (No copyright on the image)

Figure 1-2: Water-stressed basins of the world[4]. (Baseline water stress is defined as the ratio of total withdrawals to total renewable supply in each area. A darker color represents more water users are competing for limited water supplies.)



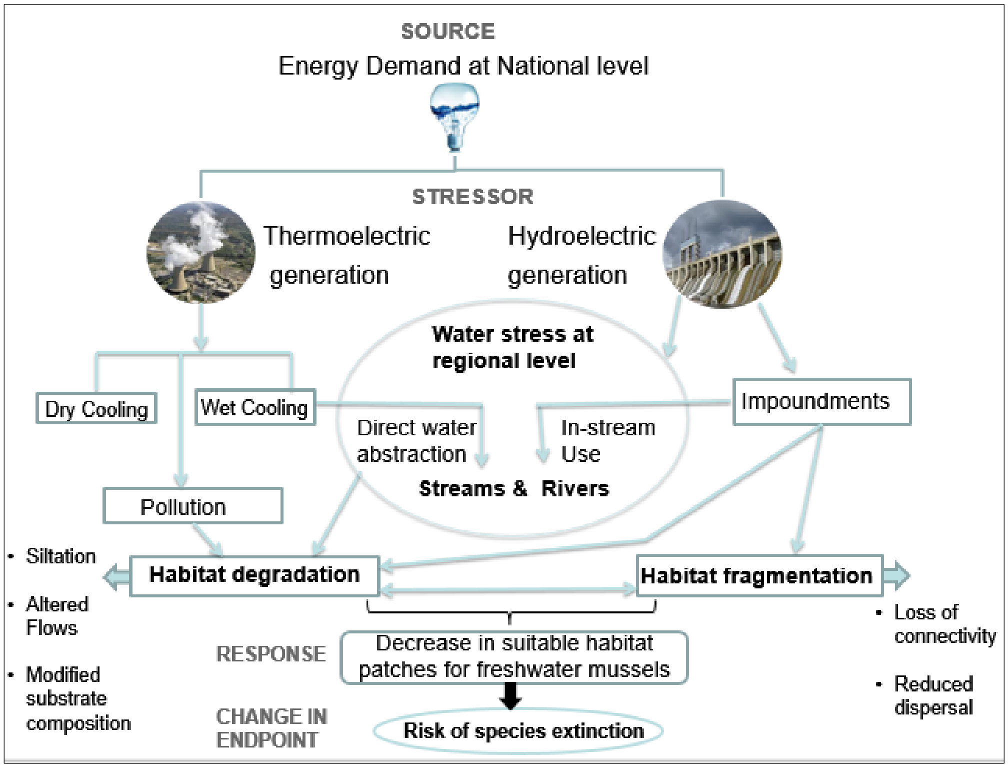
[4] Used with permission: Water stress indicator (WSI) in major basins, Source: Philippe Rekacewicz, GRID-Arendal, February 2006, https://www.grida.no/resources/5586

Figure 1-3: The unusual life cycle of freshwater mussels[5] (Wisconsin DNR).



[5] Source: Freshwater Mussels of Iowa, 2002
Illustration: Exploration of the Mississippi River, Jeff Janvrin, Mississippi River, Lower St. Croix Team, Wisconsin DNR, dnr.wi.gov/water/.../mussels/Life%20Cycle%20of%20a%20Feshwater%20Mussel.pdf

Figure 1-4: Conceptual flow-chart linking the energy sector's water demand to impact on freshwater biodiversity, specifically freshwater mussels.



CHAPTER TWO

ELECTRICITY-WATER NEXUS: A CRITICAL REVIEW OF WATER USE IN ELECTRICITY SECTOR AT THREE SPATIAL SCALES- NATIONAL, REGIONAL AND LOCAL

ABSTRACT

Freshwater is appropriated for several uses in the United States and the energy needs are increasing with rising population growth rate. Power generation, choice of cooling technologies, and fuel types are projected to face additional challenges in the future given the constraints on freshwater availability. This study offers a preliminary attempt at investigating the historical and predicted intensity of water usage statistics for traditional energy sources along with various renewable energy sources. The data is presented as water withdrawn or consumed (million m^3) by renewable and non-renewable electricity generation at the national-, regional- and local- scale. The results indicate that in US, hydropower along with fossil fuels dominate the water use in electricity sector. At a regional (South Carolina) and local scale (Savannah Basin), the water manipulation in term of instream water use is dominated by hydropower, but the freshwater consumption is largely contributed to cooling needs of the thermoelectric facilities especially those of the four major nuclear power plants. Hydroelectric sources account for most water withdrawal/manipulation at all three levels, however, thermoelectric sources dominate the water consumption. There is an apparent shift in thermoelectric generation with natural gas taking precedence over coal. This study predicts an overall increase in water consumption with water withdrawals being variable especially at local-level. In Savannah

basin, the increase in water consumption is bound to have negative repercussions on aquatic biodiversity.

Keywords: Electricity-Water Nexus, Water withdrawal, Water consumption, Aquatic Biodiversity, Savannah Basin

INTRODUCTION

Water and energy are key resources in the growth and advancement of the world economy. Freshwater is critical for life and its importance for survival is beyond measure. Historically human settlements have suffered due to lack of usable water leading to starvation, diseases and communal disharmony. Water is crucial for agriculture, drinking water and energy production all of which contribute to economic and social security. However, water is a finite and scarce resource. Freshwater accounts for only 2.53% of global water resources, of which 1.74% is locked up in glaciers and ice which leaves less than 1 % in surface and groundwater's for our availability and usage (Shiklomanov & Rodda, 2004). Overexploitation of surface and groundwater combined with global climate change has threatened the existing freshwater sources jeopardizing human wellbeing and aquatic organisms alike. Energy on the other hand is directly linked to improved living standards and economic growth across the globe. It is however increasingly becoming a water thirsty resource, with energy production supply chain in 2010 resulting in 15% of the world's total water withdrawals of which 2% was consumed and not returned to its source. (International Energy Agency (IEA), 2012). Thus, water and energy are closely linked—water being both a producer and a user of energy while energy used in every aspect of water production and supply chain (Gerbens-Leenes, Hoekstra, & Meer, 2007; Malik, 2002). Generation of electricity utilizes steam-electric technology, in which large quantities of water is used to produce steam which turns the turbines which leads to production of electricity. Similarly, large quantities of water are used for turning the hydraulic turbines to generate hydroelectric power. Thus, water security is an important factor that drives the future of energy production by deciding fuel mix, generating and cooling technologies, efficiency improvement and regulatory scenarios. The demand for energy is going to escalate owing to increase in industrial and technological demands. That combined with constrained freshwater resources is likely to threaten water security by creating a conflict between water for energy production and that for maintaining environmental flows.

Electricity-Water Nexus at the National Scale

The average annual freshwater availability in United States is 3069 billion (10^9) m^3/year of which approximately 78.60% or 2412 billion (10^9) m^3 water is withdrawn/ manipulated and 0.37% or 11281 million (10^6) m^3 water is consumed by electricity generating facilities (Dziegielewski et al., 2006; Gleick et al., 2011). Hence the overall renewable water resources in the United States seem to exceed the water use owning to temperate climate and glacial and precipitation inputs to the major river basins within the country (International Energy Agency (IEA), 2015). There are numerous uses of freshwater resources within the United States. In 2010, thermoelectric cooling was the principal user of water, accounting to 45% of water use followed by agriculture at 33%, municipal public water supply at 12% and domestic, industrial/mining, livestock and aquaculture accounting for the remaining 10% (Figure 2-1). In 2010, nearly 95 percent of net generation capacity in the U.S. is attributed thermoelectric and hydroelectric power plants. A lifecycle analysis of energy production indicates that water is needed for all phases including fossil-fuel extraction, transport and processing, generation of electricity, pollutant scrubbing, controlling air emissions and irrigation of feedstock for biofuels (Gerbens-Leenes et al., 2007). The United States, thermoelectric cooling has been the largest category of water withdrawal since 1965 (Hutson, 2004). The generation of energy/electricity requires both the withdrawal and consumption of water for cooling purposes and thus represents one of the largest demands of fresh and saline water in the United States (Kenny et al., 2009; Maupin et al., 2014). In thermoelectric power plants for cooling needs, water is diverted from the source and passed through a heat exchanger to condense the steam after it has been used to drive the turbine. According to USGS, the process of diverting the water is termed as "withdrawal" which is defined as the amount of water removed from the ground or diverted from the surface-water source, while "consumption" refers to the amount of water that is evaporated during the cooling process and hence unavailable within the watershed (Hutson, 2004). Both these categories together represent the blue water footprint for electricity generation (Hoekstra & Mekonnen, 2011; Hoekstra, Chapagain, Aldaya, & Mekonnen, 2011a)**.** In 2010, 41% of the water withdrawals were associated with thermoelectric plants, however only 2% of it is consumed (Maupin et al., 2014). Water withdrawals associated with different thermoelectric fuel types are always greater than consumption (International Energy

Agency (IEA), 2015), however both are capable of threatening energy security in times of water-stress.

Thermoelectric power plants can be powered by fossil fuels namely coal, natural gas, petroleum and non-fossil sources such as geothermal, nuclear, and biomass fuels. All thermoelectric power generation uses water for cooling purposes and for makeup water that replenishes boiler water lost through evaporation. In 2010, the US net electricity generation was 4126 million megawatt-hrs. (mMWh) (US Energy Information Administration, 2012), of which thermoelectric sources were a major contributor with the highest percentage was coal generated electricity, followed by natural gas, nuclear and renewables in that order. Currently, coal and nuclear power plants utilize the largest amount of water for electricity generation (Diehl & Harris, 2014). The thermoelectric nuclear plants have lower thermal efficiency than thermal plants powered by other fuel sources and thus have consistently higher water withdrawals and consumption (World Nuclear Association, 2017).

The water requirements for the different fuel types vary with the efficiency of the fuel source and the type of cooling system employed. There are three main types of cooling systems employed in thermally-driven electricity generating facilities. The once-through cooling systems require large volumes of water withdrawn from the water source such as rivers or reservoirs to be passed through the condenser and some portion of this withdrawn water is returned to the source at a higher temperature. The efficiency of once-through systems is higher making them widely used in thermal power plants, however it utilizes large quantities of water and causes thermal pollution (Macknick et al., 2012). Wet re-circulating systems withdraw freshwater, and pass it through a steam condenser and instead of letting the heated water back to the source, it is cooled in a wet tower or pond reducing the need to withdraw large amounts of water continuously from the source. The drawback of this cooling type is that it loses a higher percentage of water to evaporation, though the water withdrawn is almost 50 times lesser than once-through systems. Recirculating systems only withdraw deficit water to replace evaporative losses and maintain water quality. Dry cooling systems implement air flow to be mechanically driven through a cooling tower to condense steam. This requires minimal water as compared with other systems. The drawback includes high initial cost and lower efficiency in generating electricity. Their cost is about 3-4 times higher than for wet tower or pond systems, although the impact on the overall cost of the plant depends on its size and type. Because air is a less effective medium than water for cooling, dry cooling can affect power plant performance, reducing average generation and hence not suitable for a power plant with higher generating capacity (DOE/NETL, 2006; International Energy Agency (IEA), 2015). Many policy reforms are implemented by state and federal agencies to significantly reduce the energy-impact on water by utilizing advanced cooling systems such as wet towers and dry cooling, although this entails higher capital costs and reduces plant efficiency (Sanders, 2014). From Table 2-1, it is evident that the withdrawal and consumption factors show similarity when organized according to cooling technologies. Clearly, once through cooling technologies withdraw large amount of water per unit of electricity produced (100 times more than that withdrawn by recirculating technologies). In contrast, the recirculating technologies consume twice as much water as compared to the once through cooling technologies.

Hydropower contributes to 10% of the total power generated in the United States (US Energy Information Administration, 2012). It utilizes large quantities of water employed to rotate the hydraulic turbines which generate electricity and hence is a major water manipulator and consumer due to water being evaporated or lost to seepage (Mekonnen & Hoekstra, 2012). Factors determining the amount consumed – climate, reservoir design and allocations to other uses – are highly site-specific and variable. By one estimate, hydropower facilities consumption factors fall into a wide range that depends on the type (impoundment/run-of-river/pumped storage) /design/volume of the facility and the climate (Torcellini, Long, & Judkoff, 2003). Hydropower plants operating with large reservoirs are more susceptible to evaporative losses than run-of-river hydroelectric plants which store little water leading to near zero evaporative losses. Electricity generated from non-hydro renewable resources such as concentrated solar power (CSP), wind, geothermal and photovoltaic (PV) systems is associated with smallest withdrawals which are equivalent to the consumption factors (Macknick, Newmark, Heath, & Hallett, 2012; Torcellini et al., 2003)**.** Based on Table 2-1**,** the renewables such as wind and photovoltaic have low water use as well as less carbon dioxide emissions. The bioenergy and hydroelectric power have high water use and low carbon emissions.

Thermoelectric and hydroelectric power plants have significant environmental impacts on freshwater ecosystems and have been a cause for declines in aquatic biodiversity in the recent decades (Dudgeon et al., 2006; NETL, 2009b). In thermoelectric power generation, the cooling water evaporates leading to minerals and other suspended impurities being concentrated in the boiler feed. The thermally contaminated water is discharged in surface water sources altering the water temperatures, flow volume and timing and reducing the concentration of dissolved oxygen having several implications on aquatic organisms such as endemic fish and mussel species (International Energy Agency (IEA), 2012; McDonald et al., 2012; Nedeau, Merritt, & Kaufman, 2003). Hydroelectric dams are associated with numerous environmental and social impacts though it is touted as a relatively clean, low-cost and renewable form of energy (Herath, Deurer, Horne, Singh, & Clothier, 2011). Hydroelectric dams have substantial ecological consequences apart from increasing the rate at which water is lost by evaporation by converting lotic systems to lentic ones. They also cause fragmentation of riverine habitat causing loss of biological connectivity and altering hydrologic regimes thereby imperiling aquatic biota (Anderson, Pringle, & Freeman, 2008; Craig, 2000; McAllister, Craig, Davidson, Delany, & Seddon, 2001; Pringle, Freeman, & Freeman, 2000). Both hydroelectric and thermally powered plants are known to cause fish kills due to entrainment (pulling through the cooling process) and impingement (trapping against a screen) (Averyt et al., 2011). Several freshwater biota are on a fast track to extinction due to many anthropogenic causes of which imperilment by presence of dam and loss of habitat are the primary ones (Larsen, Williams, &

Kremen, 2005; Ricciardi & Rasmussen, 1999; Williams et al., 1993). The estimated increase in energy generation to meet the demands of population increase as well as economic growth is likely to increase water demands over the next few decades and worsen the current aquatic biodiversity crisis.

Electricity-Water Nexus at the Regional and Local Scale

Unlike the overall national water situation in the United States, the regional water scenario is very diverse and unpredictable. Water is infrequent in the dry southwest and is a key concern for electricity generation. Similarly, though southeast appears plentiful in terms of water resources, high population growth in recent decades has created increased electricity needs with subsequent increases in water use. For example, droughts in the southeast in 2007 and 2010 curtailed operations to conserve water and reduced output from hydroelectric and thermal power plants (Besse et al. 2012). Elsewhere in the United States, electricity generating facilities are susceptible to blackouts due to irregular water availability triggered by climate changes which increases the risk of environmental catastrophes such as droughts, floods, heat wave and hurricanes.

In the south-east, South Carolina appears to be the most extreme cases of underreporting both water withdrawals and consumption (Averyt et al., 2011). Several watersheds in the southeast are a biodiversity hotspot with at least 10 or more mussel and fish species at risk exemplifying the diverse species diversity within the streams and rivers. (Lydeard & Mayden, 1995; Master, Flack, & Stein, 1998; Williams et al., 1993). Several states including South Carolina harbor watersheds (namely Catawba and

Savannah basins) where there are competing needs between power plants and aquatic fauna resulting in water-supply stress (Averyt et al., 2011; SC DNR, 2015). South Carolina is ranked third in the nation in nuclear generating capacity and annual generation with the surplus electricity being exported to other states. Naturally, nuclear energy is the highest generator of electricity in this state, with Oconee nuclear power plant being the state's largest power plant. There are 8 major river basins within South Carolina; Broad, Catawba, Edisto, Pee Dee, Salkehatchie, Saluda, Santee and Savannah river basins. Several watersheds within these basins support at-risk native fish and mussel species (Alderman, 1998; SC DNR, 2009). The power plants in such a prime habitat of endangered and threatened species is likely to appropriate water resources away from its instream purpose critically imperiling the aquatic biota. The Savannah river basin, the second largest in the state, is one such basin harboring both a rich diversity of threatened species and there are several reports on understating the water use by these power plants to the EIA, including that on Seneca river within the Savannah Basin in South Carolina (Averyt et al., 2011) which acts as the primary supply of cooling water to the Oconee Nuclear Power plant run by Duke Energy Carolinas, LLC (US Energy Information Administration, 2015.).

The Savannah River Basin is an ecologically and economically valuable resource. It drains approximately 27,395 km^2 of area in the states of Georgia, North Carolina and South Carolina, of which 12,691 km^2 lies in the state of South Carolina square miles, and occupies 15.8 % of the State's area. The Savannah River is now a major water resource providing municipal and industrial water and act as an important source of power generation in the southeastern United States. Majority of the mainstem Savannah river as well as a few tributaries are impounded causing loss of free-flowing riverine habitat and causing change and fluctuations in the quality and quantity of flow regimes. Five major hydroelectric facilities (Figure 2-1) are the Hartwell Dam, Richard B. Russell and J. Strom Thurmond (built by US Army Corps of Engineers) and Keowee & Jocassee Dams (built by Duke Energy). Amongst the thermoelectric facilities, the Oconee nuclear facility (Figure 2-2) located on Lake Keowee, in Seneca, SC is owned by Duke Energy and is one of the nation's largest nuclear plants with a generating capacity of approximately 2.6 million kilowatts (Barzack et al 2007 & Duke Energy).

The Savannah basin harbors diverse endemic aquatic fauna. The mainstem of the Savannah River and its tributaries are home to the robust redhorse (*Moxostoma robustum*) and federally endangered shortnose sturgeon (*Acipenser brevirostrum*) as well as at least 15 priority fish species such as christmas darter (*Etheostoma hopkinsi*), redeye bass (*Micropterus coosae*), Savannah darter (*Etheostoma fricksium*) and turquoise darter (*Etheostoma inscriptum*) (Master et al., 1998). Several priority mussel species such as barrel floater (*Anodonta couperiana*), pod lance (*Elliptio folliculata*), roanoke slabshell (*Elliptio roanokensis*), yellow lampmussel (*Lampsilis cariosa*), rayed pink fatmucket (*Lampsilis splendida*) and Savannah lilliput (*Toxolasma pullus*) are also found in the mainstem Savannah River (SC DNR, 2015). The Comprehensive Wildlife Conservation Strategy for the State of South Carolina identifies Stevens Creek and Turkey Creek watersheds as critical habitats for several mussels the brook floater, yellow lampmussel, creeper and the federally endangered Carolina heelsplitter as priority species (SC DNR, 2015). The hydrologic alteration and the water appropriation by power plants have significantly affected this aquatic fauna of the mainstem Savannah river and its tributaries.

Research Objective

Several studies have conducted an extensive consolidation of literature on water use factors by electricity generating technologies taking into consideration the various cooling systems employed by these technologies (Dziegielewski et al., 2006; Fthenakis & Kim, 2010; Gerbens-Leenes et al., 2007; Gleick, 1994; Inhaber, 2004; Macknick et al., 2012). The goal of this article is to incorporate the above-mentioned literature to create a realistic temporal snapshot of the water use in electrical production as we are trying to sustain our water and energy resources. Many watersheds in the United States (U.S.) are already running out of water to utilize—especially in the Southeast (Sovacool, 2009). This study will provide estimates of annual water withdrawn and consumed (million m^3) by net electricity generated by different electricity producing carriers namely coal, natural gas, nuclear fuel, geothermal, hydropower, solar and biofuels (blue water footprint; WF_{blue}) at the different spatial scales; national, regional and local-level in order to understand how future energy scenarios will affect the water resources use and identify management practices and research strategies to address current and emerging water-energy conflicts.

METHODS

Compiling Electricity Data

This paper focuses on estimating water use exclusively during the operational phase, and does not address full lifecycle assessment of water use in electricity production. Full lifecycle assessments involve estimates of water use in the mining operations, fuel processing, transportation, irrigation of bioenergy crops and cooling processes. The operational phase includes water utilized in cleaning, cooling and other processes that occur during the electricity generation such as blowdown of boilers, wet scrubbing and flue gas desulphurization (Hoffmann, Forbes, & Feeley, 2004). It is a general consensus that most of the dominant water use using majority of fuel types in electricity generation occurs during the operational phase with the exception of using biomass as a fuel type (Fthenakis & Kim, 2010; Macknick et al., 2012). Apart from this, it is difficult to obtain reliable data on other aspects of water use such as fuel processing, as much of the fuel is processed elsewhere and would have water stress implications at the specific regional water resources. Hence, in this study, we limit our analyses to water use during the cooling process of the operational phase of electricity production/generation by various fuel type. The net electricity generated in segregated into nine electricity generating fuel types namely; coal, natural gas, nuclear, petroleum, conventional hydropower, geothermal, solar, wind, other renewables including wood, wood-waste and biomass, based on the sectors used in the Annual Energy Outlook 2012 (US Energy Information Administration, 2012). For the sake of convenience, the conventional electricity producing sources are coal, natural gas and nuclear. The nonconventional sources are categorized as ‘Hydroelectric facilities’ and ‘Other Renewables’ consisting of solar, wind, geothermal and biomass. We compiled the net electricity generated from 1950 till 2016 and the future reference case scenario till 2035 from the Department of Energy’s Annual energy outlook (AEO) reports (US Energy Information Administration, 2012). The energy scenarios to be considered for the analysis would be the Reference Case by EIA’s Annual Energy Outlook which are business-as-usual trend estimate assuming that current laws and regulations are maintained throughout the projections. Thus, the projections provide policy-neutral baselines that can be used to analyze policy initiatives with a baseline economic growth (2.5 percent per year from 2010 through 2035).

Calculating Water Use in Electricity Generation

There are several ways for accounting water requirements of different industrial, agricultural and municipal processes. For this paper, we define and measure water use (any surface or groundwater used to generate electricity) as United States Geological Survey does, by segregating into two sub-categories; water withdrawal and consumption. Water withdrawn is defined as the amount of water removed from the ground or diverted from the water source, while consumption refers to the amount of water that is evaporated, transpired, incorporated into products or crops, or otherwise removed from the immediate water environment (Kenny et al., 2009). Our definition of water use borrows from the concept of blue water footprint, a partial concept that makes the tool

Water Footprint which is a comprehensive indicator of freshwater resources appropriation quantifying not only direct water use of a consumer or producer, but also the indirect water use. It consists of three categories; blue water (consumptive use of surface and groundwater), green water (consumptive use of rainwater) and grey water (volume of water polluted) (Hoekstra, Chapagain, Aldaya, & Mekonnen, 2011b).

For all thermal electricity generating facilities the water withdrawal and consumption will vary with the fuel type (coal, natural gas, nuclear) and the cooling technology (once-through, wet cooling and dry cooling) employed. According to the US Geological Survey, hydroelectric power generation does not withdraw water or divert water flow, and is categorized as 'instream' water use. The actual water consumption in case of hydroelectric facility would be the evaporative losses resulting from the water storage in a reservoir. For our analysis, we calculate the in-stream water use as a volume of water that is circulated through the hydraulic turbines as water withdrawal by considering it as a manipulation of the natural course of the water body. Hence in case of hydroelectricity it will be termed as water manipulation instead of water withdrawal (McDonald et al 2012). For the other renewable fuel types, such as solar, wind and geothermal, the water withdrawals are assumed to be equivalent to consumption. We then consolidated the published estimated water- use factors for electricity generation techniques based on fuel types and cooling technologies from several published reviews and analyses (Dziegielewski et al., 2006; Fthenakis & Kim, 2010; Gerbens-Leenes et al., 2007; Gleick, 1994; Inhaber, 2004; Macknick et al., 2012). This compiled information provides median, minimum, and maximum water use coefficients (gallons per megawatt-hour, or MWh) at the generator scale to calculate the range of possible water withdrawals and consumption.) We used the median water use coefficients as the purpose of this study was to gain an understanding of how water use changes with change in fuel types and use of cooling technologies temporally and spatially. For our study, first we converted the water use factors from gallons per megawatt-hour (gal/kWh) to cubic meters per kilowatt-hour (m^3/kWh, then we multiplied these median water-usage statistics by the net electricity generated estimates to obtain the average estimates for total annual water use (million m^3) in terms of withdrawals and consumption. Table 2-2 provides the statistics on water withdrawal (m^3/kWh) and consumption factors (m^3/kWh) based on fuel types and cooling technologies.

Temporal and Spatial analysis of Water Use

The temporal trend in electricity production from 1950 to 2010 and projected trend till 2035 were determined by using the sector wise annual data compiled using the Annual Energy Outlook's 2012 reference case forecast for electricity generating capacity (Table A8; (US Energy Information Administration, 2012)), and the future freshwater requirements for both thermoelectric and renewable technologies were estimated and compared to current and past water use by the electricity sector. The temporal trend with projections of water use till 2035 were applied to net electricity generation at the national level i.e. United States as the data is readily available for such projections. At the regional scale and local-scale, i.e. South Carolina and the Savannah Basin, net electricity generation data are not readily available from the EIA prior to 2001 and hence the temporal trend explored at the regional- and local- level were assessed from 2001- 2016, as no future projections are available at this scale. In case of Savannah Basin, this study attempts to gather improved power plant level data on both withdrawals and consumption by applying the appropriate cooling technology and fuel type water factors to the corresponding power plants that appropriate water resources within this basin. The primary details about the electricity facilities such operator, the fuel type, design/technology and generating capacity of facility are provided in Table 2-3. Future energy scenarios within the basin with a focus on water conservation and resource sustainability will be considered for policy recommendations. This study will help plan for future electricity scenarios and water-electricity policy analysis at a regional level and for maintaining the ecological integrity of the Savannah River Basin. In conclusion, we compared our calculations of water withdrawals and consumption based on the coefficients summarized in Table 2-2 with withdrawals and consumption reported by the EIA and state agencies. and the withdrawals from thermoelectric power plants reported by the U.S. Geological Survey (USGS) in 2010 (Maupin et al., 2014) the most recent five-year water census from USGS.

RESULTS

Trends in Electricity Production

Historically, there was predominance of fossil-fuels in the domestic net electricity generation, with coal contributing to more than 50% of net electricity generated till 2005. The current electricity production at the national-level is dominated equally by coal and natural gas with supplements from nuclear and hydroelectricity (Figure 2-3). By 2035, the Reference Case predicts an increase in net electricity generation with the annual growth rate of electricity generation between 2010 and 2035 being 0.6% (Figure 2-3). There is a rise in electricity generation from all fuel sources, particularly natural gas and nuclear fuel with a consistent decrease in coal. Amongst renewables, conventional hydropower's contribution in the net electricity generation varies from year to year depending on rainfall, runoff and many factors that play a role at regional scale such as droughts and floods. The peak of hydropower generation was in 1995 when it contributed about 9% to all US electricity generated and has since been on a downward trend (Figure 2-3). Since 2010 based on the reference scenario forecasts by the Annual Energy Outlook 2012, in accordance with the current federal policies, there is a rise in the contribution of renewable energy sources to the net electricity generation at the national scale, particularly in wind energy and biomass (Figure 2-3). The rise in the net domestic electricity generation seems to falter owing to the extended policies case which predicts a similar combination of fuel sources as reference case, but with overall reduced population growth combined with increased energy efficiency (US Energy Information Administration, 2012).

The net electricity generation at regional-level in South Carolina was 2.5% of the total US domestic electricity generation in 2015. Since 2001, nuclear power has contributed to more than 50% of net electricity generated within the state. The current electricity production is dominated by nuclear with supplements from coal, natural gas and hydroelectricity in that order (Figure 2-4). In 2016, the state's 4 nuclear facilities

Oconee and Catawba Nuclear power plants operated by Duke Energy Carolinas, LLC; V C Summer operated by South Carolina Electric and Gas company and H B Robinson by Duke Energy Progress contributed to 58% to the state’s net electricity generation. In the past decade, majority of South Carolina’s electricity was generated by coal-fired thermal plants, but now those plants supply about half as much electricity as they earlier did. In contrast, since 2007 the natural gas contribution to South Carolina's electric power sector have almost tripled in the past decade. The remaining electricity generation was attributed to renewable resources, including conventional and pumped hydroelectric power plants, biomass-fueled facilities that use wood waste or methane, and solar energy and in 2016 the majority of it comprised of conventional hydroelectric power and biofuel generation (Figure 2-4). There are more than 20 small and large hydroelectric power plants in South Carolina, including several large pumped storage facilities. Most of the hydroelectric facilities are based in the western part of the state, primarily impounding the mainstem Savannah river (Figure 2-2). In South Carolina, the annual growth rate in electricity generation from 2015 to 2016 was 0.6%. Also, in South Carolina the net generation is higher than the consumption and the surplus electricity is exported to other states (US Energy Information Administration, 2015.)

Since 2001 the net electricity generation at local-scale in Savannah river basin is dominated by the Oconee nuclear power plant generating more that 60% of the net electricity within the basin. The rest of the electricity is generated by a mix of natural gas fueled power plants John S Rainey, Urquhart, Jasper and hydroelectric plants J Strom Thurmond, Keowee and Rocky River (Figure 2-5). In 2016, the Oconee nuclear plant operated by Duke Energy Carolinas, LLC contributed to 65% of the net electricity generated within the Savannah basin. The only coal-fired power plant in the basin contributed to almost 9% of net electricity generated till 2012. However, it was decommissioned in 2013 and replaced with a much cleaner fuel type, natural gas. This is consistent with the trend in the US and in South Carolina with the rise in the contribution of natural gas as a fuel type in electricity generation. In 2015-2016, the renewable energy sources contribute to approximately 2.5 % of the net electricity generation with the majority being generated by hydroelectric facilities namely, J Strom Thurmond, Keowee and Rocky River and a biomass facility, Savannah River Site which utilizes a combination fuel type of wood waste and landfill gases (Figure 2-5).

Trends in Water Use in Electricity Generation

Within thermoelectric generation, the cooling systems employed are more responsible for determining the water use in electricity generation that the various fuel sources utilized such as coal, natural gas, nuclear fuel and biomass/biofuels. The once-through cooling technology withdraws higher quantities of water as compared to the recirculating towers/ponds. Dry cooling technology withdraws the least amount of water for any fuel type. Amongst fuel types, nuclear power has higher water withdrawal rates followed by coal, biomass/biofuel and natural gas-powered electricity generation, in that order (Table 2-2). Between renewables, there is a huge disparity in water withdrawals. Based on the consolidated published reviews, the highest water withdrawal happens to be the water manipulation owing to hydroelectric generation. On an average, the factor is at least 3 orders of magnitude more than the withdrawal factors for the other fuel types.

The water consumption patterns show similar trend as that observed in water withdrawal/manipulation. In thermoelectric power generation, the cooling technologies impact the water consumption more than fuel type. For once-through cooling technology the water consumption factor is at least one order of magnitude less than the recirculating towers and cooling ponds. Within fuel types, nuclear and coal power consumes more of the withdrawn water than natural gas and biofuels/biomass. Consistent with the withdrawal factor, hydroelectric power loses largest quantities of water to produce electricity via evaporation and seepage and is the largest water consumer in electricity generation. Amongst other-renewables, the water consumption is equivalent to water withdrawal factors and are very low in the range of 10^{-6} m^3/kWh for solar and wind and 10^{-3} m^3/kWh for geo-thermal technology which is consistent with the cooling requirements of a thermally driven power plant (Table 2-2).

In US, hydropower consistently ranks first in annual average water withdrawals, with 994,728 million m^3 withdrawn in 1950 and 2,131,776 million m^3 in 2015. The next highest water withdrawer is coal (6142 million m^3 in 1950 to 62840 million m^3 in 2015), followed by nuclear power (0 million m^3 in 1950 to 54983 million m^3 in 2015) and natural gas (1307 million m^3 in 1950 to 33151 million m^3 in 2015). In the reference case forecast, coal is predicted to withdraw 75,400 million m^3 of water as compared to nuclear power which will withdraw 58,760 million m^3 of freshwater and natural gas which will withdraw 41,013 million m^3 of freshwater by the year 2035 (Figure 2-6). The overall average water withdrawals in the United States has increased from 1,002,178 million m^3 in 1950 to 2,282,750 million m^3 in 2015 with an increase of 128%. Figure 2-3 shows an upward trajectory in water withdrawals from 1950, with the peak being in 1995 owing to the higher percentage of electricity generation by hydroelectric power and eventually decreasing to the lowest withdrawals in 2010 followed by a slight upward trajectory from 2015 to 2035. The reference case scenario predicts that from 2010 to 2035 the annual overall water withdrawals are going to increase by 21% with increase in electricity generation by hydroelectric, natural gas, nuclear and bio-fuels (Figure 2-3).

In the US, hydropower consistently ranks first with annual average water consumption, with 2,362 million m^3 of ^{water} consumed in 1950 and 5,062 million m^3 in 2015.The water consumption by hydropower is predicted to increase by 4.94% from 2015 to 2035. The next highest water consumer is coal with an annual average water consumption of 240 million m^3 in 1950 and 2453 million m^3 in 2015, followed by natural gas with 38 million m^3 in 1950 to 954 million m^3 in 2015 and nuclear power with 0 million m^3 in 1950 to 1623 million m^3 in 2015. There has been a substantial rise in overall average water consumption in the United States from about 2,640 million m^3 in 1950 to 10,142 million m^3 in 2015 with a predicted increase of 11,281 million m^3 water consumed in 2035 (Figure 2-6). There was a noticeable decline in water consumption between 2000 to 2010, with an upward trajectory from 2015 till the forecasted 2035. The reference case scenario predicts that the annual water consumption in the United States is going to increase by 17 % from 2010 to 2035 to sustain the electricity generation. Since most of the thermoelectric cooling technologies and fuel types have consumption factor in similar ranges, the annual water consumption will not be affected with a change in policy scenario regarding decommissioning of coal or incentives for natural gas use. The predicted annual water consumption will however increase if there is boost in the use of hydroelectricity (Figure 2-3 and Figure 2-6).

In South Carolina, water withdrawals by hydropower consistently ranks first in annual average water withdrawals, with 8,787 million m^3 withdrawn in 2001 to 17,208 million m^3 in 2016 (Figure 2-7). The next highest water withdrawer was nuclear power (3,304 million m^3 in 2001 to 3,698 million m^3 in 2016), followed by coal (1,459 million m^3 in 2001 to 835 million m^3 in 2016), natural gas (34.5 million m^3 in 2001 to 475 million m^3 in 2016) and bio-power namely, bio-fuels and bio-waste (41 million m^3 in 2001 to 109 million m^3 in 2001). The water consumption patterns by electricity generation in South Carolina differs from the withdrawal patterns. According to 2-7, the ranking of energy sources in attributing to current water consumption are led by nuclear (98 million m^3 in 2001 to 110 million m^3 in 2016), coal (57 million m^3 in 2001 to 33 million m^3 in 2016), hydropower (21 million m^3 in 2001 to 41 million m^3 in 2016), natural gas (1 million m^3 in 2001 to 14 million m^3 in 2016). If the trend continues in the future, the water consumption trend in South Carolina will be on an upward trajectory with more contributions from nuclear power and natural gas (Figure 2-4 and Figure 2-7)

The water use patterns in Savannah Basin vary temporally. The water use by thermoelectric facilities namely coal and natural gas fueled power plants is steady with slight increase and decrease. The water use by hydroelectric facilities is highly variable with no apparent trend and that by other renewables is on a slight upward trend, predominantly due to use of wood-waste and biofuels (Figure 2-5, Figure 2-8, Figure 2-9). From 2001 till 2016, the highest withdrawals are associated with the hydroelectric facilities namely, J Strom Thurmond, Keowee and Jocassee and Bad creek which are pumped storage facilities. The combined hydroelectric facilities contributed to approximately 21,000 million m^3 of instream water use which attributes to manipulation of the aquatic systems these reservoirs are built upon. These hydroelectric facilities consume between 19 to 30 million m^3 of water which is 0.14 % of the water withdrawn/manipulated. From 2001 till 2016, the second highest water withdrawals are by Oconee nuclear facility which has been consistently withdrawing between 3,200 to 3,555 million m^3 of water from the Keowee lake. The Oconee nuclear facility consumes between 19 to 22 million m^3 of water, which accounts to 0.62% of the water withdrawn. Between 2001 to 2016, the natural gas plants, namely Urquhart, John S Rainey and Jasper withdrew approximately 95 to 588 million m^3 of water and consumed 0.3 to 5.2 million m^3 of water, which is 0.88% of the water withdrawn. The only bio-power plant in the basin, Savannah River Site facility withdrew 10 million m^3 of water and consumed 0.8% of the withdrawn water (0.08 million m^3, Figure 2-8, Figure 2-9).

DISCUSSION

It is evident from this study that fossil fuels dominate the U.S. energy generation. At the regional and local scale, South Carolina and Savannah Basin respectively, nuclear power precedes any other energy source in electricity generation. In Reference case predicted electricity forecast, there is a gradually shift to lower-carbon options such as natural gas, wind and other renewables. Though the national-level water withdrawal and consumption is dominated by hydroelectricity, the thermoelectric water use will be affected mostly by changing policies and regulation. At the national-level, our estimated thermoelectric water withdrawals in the year 2015 are 1,50,974 million m^3 as compared to water withdrawals reported by EIA in 2015 is 2,33,881 million m^3 and those modeled by USGS for 2010 are 1,77,755 million m^3. The thermoelectric water consumption estimated by our study in 2015 is 5,031 million m^3 and that reported by EIA is 3,995 million m^3. According to our estimates the water consumed is approximately 3% of the water withdrawn as compared to the EIA estimates which is 1.7% of the water withdrawn. There is clearly a discrepancy in the consumption reporting as previously noted by studies where they noted that several power plants underreport or misreport the total volume of water consumed and withdrawn annually (Averyt et al., 2013; Averyt et al., 2011).

In South Carolina, these under-reporting of total water use is very common and to show the discrepancies in water use, we compare estimates generated by this study to that with the EIA 923 Forms and the database generated for a study conducted by Union of Concerned Scientists[6] (UCS, 2011). According to our estimates, in 2008, thermoelectricity generation in South Carolina withdrew 5331 million m^3, the EIA

[6] *Union of Concerned Scientists. 2012. UCS EW3 Energy-Water Database V.1.3. www.ucsusa.org/ew3database*

reports 1160 million m^3 and UCS calculated 8839 million m^3. Our estimates of annual water consumption are 170 million m^3 and those reported by EIA are 75 million m^3 and calculated by UCS was 156 million m^3. Our estimates were close to those calculated by the UCS study and affirms the fact that power plants in South Carolina are negligent with their reports of water use to the EIA, which could affect the way decisions regarding management of water resources are enforced in times of crisis such as the droughts of 2006 and 2010 (Besse, Brendlinger, Cook, & Kelley, 2012). Since 2002, EIA did not mandate the nuclear facilities to report plant and generator based information. This accounts for the discrepancies in the EIA reported water use data since majority of water consumed by electricity sector in South Carolina is by nuclear power plants. This fallacy was corrected by EIA when a new rule was introduced to collect improved data for power plants (including nuclear and thermoelectric renewables) and needed them to report water use from 2010 onwards (Averyt et al., 2013). On the other hand, though there are several hydroelectric plants in South Carolina, approximately only 2% of the electricity is generated by them as they are peaking power plants, operating only when the demand of electricity is highest, especially during hot summer days. However, the water uses by the hydropower both in terms of manipulation of streams and evaporative consumptive losses is a concern.

The Savannah Basin has the greatest reported water use (both withdrawals and consumptive) amongst the eight basins in South Carolina. There are 9 hydroelectric facilities in the Savannah Basin of which five (Bad Creek pumped-storage, Jocassee pumped-storage, Keowee, J. Strom Thurmond and Rocky River) are mentioned in EIA's

State profile as contributing to hydroelectric generation in South Carolina. The two-major hydroelectric facilities Hartwell and Richard B Russell operated by Corps of Engineers, though impounding the mainstem Savannah river, are administratively located in Georgia (US Energy Information Administration, 2015.) In 2006, water manipulated (in-stream use) by the hydroelectric facilities reported by state agencies was 29,851 million m^3 which is close to our estimates 22450 million m^3 (SC DNR, 2009). In the Savannah basin, the three major thermoelectric facilities Duke energy's Oconee power plant, Santee Cooper's John S Rainey and SCE&G's Urquhart Station account for the for 97% of non-hydroelectric freshwater withdrawals of which 2% was consumed (SC DNR, 2009). Apart from water appropriation, the Oconee nuclear station causes thermal pollution in the Keowee river/lake which acts as the water source for cooling needs. In this region (watersheds in SC), the difference in the intake and outlet summer temperature due to thermoelectric plants could be as much as 14 to 16 ºC during hot summer days (Averyt et al., 2011; Besse et al., 2012). The thermal discharges have multiple impacts on local aquatic ecosystems, especially during the summer months when species are at or near their heat tolerance thresholds. This combined with a drought like condition such as during 2007-2009 drought when 30% of the southeastern region experienced exceptional drought conditions may force several power plants to halt their electricity generation (Madden, Lewis, & Davis, 2013; Sovacool & Sovacool, 2009).

The Savannah basin provides aquatic habitats for numerous aquatic biota, including at least thirty priority fish species, nine priority mussel species and 2 priority crayfish species (NatureServe., 2010; SC DNR, 2015). Several of these fish species are endangered categorized globally as critically imperiled (G1), imperiled (G2) and threatened (G3) (NatureServe., 2010). The Savannah basin has at least 40 counts of G1+G2+G3 aquatic species and an average T_{pout} (outflow water temperature) of 37 - 40 °C from the once-through cooling facility of Oconee nuclear power plant in 2001–2005 (Madden et al., 2013). Several studies have highlighted the risk of impoundments and high temperature discharges to freshwater biota especially freshwater mussels (Dudgeon et al., 2006; Williams et al., 1993). Of these a few studies have assessed the direct impacts of electricity-water nexus on aquatic species concluding that small range aquatic organisms are at risk in watersheds where the electricity sector associated water use is high (Madden et al., 2013; McDonald et al., 2012). The high priority freshwater biota occurring in Savannah Basin, e.g. freshwater fish such as darters and shiners and mussel species such as Brook Floater, Carolina Heelsplitter, Savannah Lilliput and Yellow Lampmussel are highly localized having a dispersal range of a maximum 300 meters (Schwalb, Cottenie, Poos, & Ackerman, 2011). With such high level of biodiversity and endemism combined with high water consumption and high discharge temperatures from cooling facilities makes the aquatic biota in Savannah Basin highly susceptible to imperilment.

The shifts in electricity- water nexus will occur due to several possibilities, namely, changes in fuel preference, changes in cooling practices, changes in environmental regulations, climate change and changes in electric power grid (Sanders, 2014). E.g. a choice of less-carbon intensive electricity mix could either lead to an increase or decrease in water use depending on the fuel fix and cooling technologies.

Vice versa, federal and state policies regulating water quality and quantity can have an impact on the choice of combination of technologies and energy/fuel sources to be employed to generate electricity. Accounting for all the various scenarios, the general trend leans towards a higher water consumption by the electricity sector from 2015 to 2035, while the trend of withdrawals is more variable. Decisions regarding water resource conservation and management are made are several spatial scales ranging from national level to local/watershed level often having overlapping responsibilities (Feldman, Slough, & Garrett, 2008). This study analyzed the water use and consequent water stress at three different spatial scales and identified the trends in water use that ought to be seen in the future to plan and manage our water resources sustainably. The current trend in electricity sector is highly water consumptive and in need of water-conserving/efficient technologies. We recommend the use of newer renewable energy sources such as bio-fuels, hydrogen, solar and wind which have low water consumptive factor to be a part of the future electricity-generating mix. We also suggest adopting integrated basin-scale management and integrating it with national-scale water policies to tackle issues regarding water use by electricity sector. The impacts of ecological, climatic and socioeconomic factors on local, regional and national scale will be an important aspect to incorporate in any further analyses of electricity-water nexus.

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Table 2-1: Model depicting the relationship between water use and carbon dioxide emissions[7].

CO_2 emissions ↑ (Low → High) / Water Use → (Low → High)	Low		High
High	Thermoelectric Dry Cooling	Thermoelectric Once through	Thermoelectric Cooling tower/pond
	Photo voltaic	Geothermal Cooling ponds/towers	Bio-fuels, Hydroelectric
Low	Wind and Concentrated Solar Power	Thermoelectric Combined cycle with CCS	Nuclear

[7] Macknick, J., Newmark, R., Heath, G., & Hallett, K. (2012). Operational water consumption and withdrawal factors for electricity generating technologies: A review of existing literature. *Environmental Research Letters, 7*(4), 045802.

Table 2-2: Water consumption and withdrawal factors for various electricity generating technologies.[8]

Fuel Type	Cooling types	Consumption factor for cooling type (Median) (m^3/kWh)	Average consumption factor for Fuel type (m^3/kWh)	Withdrawal factor for cooling type (Median) (m^3/kWh)	Average withdrawal factor for fuel type (m^3/kWh)
Renewable:					
Photovoltaic	Utility PV	3.78×10^{-6}	**3.78×10^{-6}**	N/A	**N/A**
Wind	Wind Turbine	3.78×10^{-6}	**3.78×10^{-6}**	N/A	**N/A**
CSP	Tower	3.41×10^{-3}		N/A	**N/A**
(concentrated solar power)	Dry	1.89×10^{-4}	**1.51×10^{-3}**	N/A	**N/A**
	Hybrid	9.46×10^{-4}		N/A	**N/A**
Bio-power	Once-Through	1.13×10^{-3}		0.132	
	Pond	1.51×10^{-3}	**9.27×10^{-4}**	1.7×10^{-3}	**4.6×10^{-2}**
	Dry	1.32×10^{-4}		3.03×10^{-3}	
Geothermal	Tower	5.67×10^{-5}		N/A	**N/A**
	Dry	9.46×10^{-4}	**9.16×10^{-4}**	N/A	**N/A**
	Hybrid	1.74×10^{-3}		N/A	**N/A**
Hydropower	Hydraulic Turbines	1.70×10^{-2}	**1.70×10^{-2}**	7.17	**7.17**
Non-Renewable:					
Nuclear	Tower	2.54×10^{-3}		4.16×10^{-3}	
	Once-Through	1.02×10^{-3}	**1.96×10^{-3}**	0.168	**6.62×10^{-2}**
	Pond	2.31×10^{-3}		2.67×10^{-2}	
Natural Gas	Tower	1.82×10^{-3}		2.38×10^{-3}	
	Once-Through	6.44×10^{-4}	**8.44×10^{-4}**	8.78×10^{-2}	**2.81×10^{-2}**
	Pond	9.08×10^{-4}		2.23×10^{-2}	
	Dry	7.57×10^{-6}		7.57×10^{-6}	

[8] Withdrawal and consumption rates within a technology category for the fuel source have been adapted from Tables 1, 2 and 3 in *Macknick et al. 2012*; from Table 1 and 2 of *Sanders, 2015* and Table 2 and 3 from *Torcellini et al 2003* (NREL Report).

Coal	Tower	2.35×10^{-3}		2.99×10^{-3}	
	Once-Through	5.68×10^{-4}	**1.55×10^{-3}**	0.108	**5.60×10^{-2}**
	Pond	1.74×10^{-3}		5.70×10^{-2}	

Table 2-3**:** Major Electricity producing facilities[9] in the Savannah River Basin.

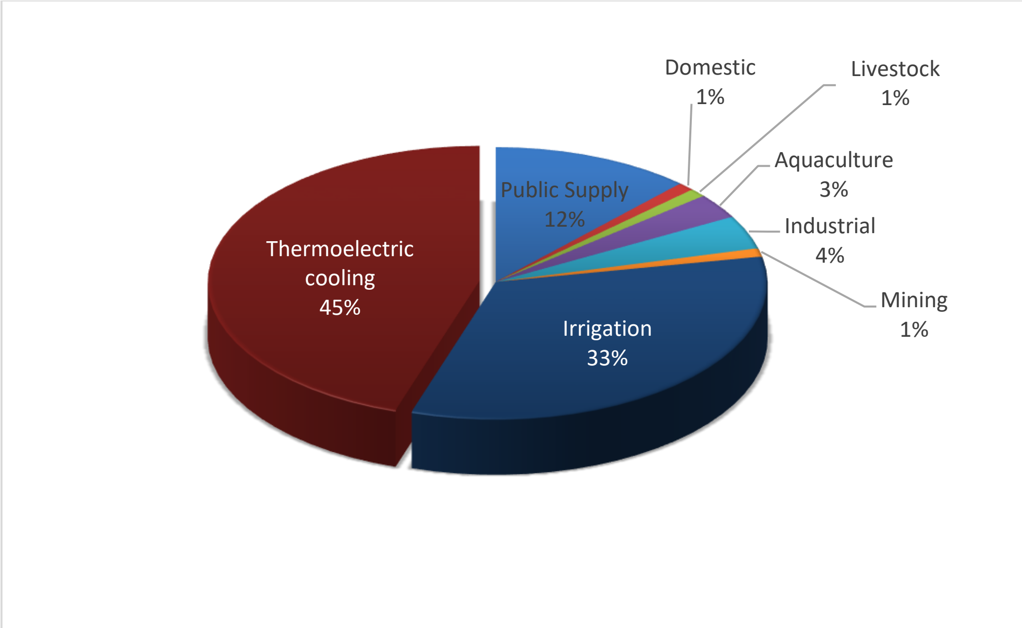
Power Plant[10] Name	Operator	Source/Fuel Type	Net electricity generation	Technology	Cooling type
Oconee	Duke Energy Carolinas, LLC	Nuclear (PWR-3)	2,554 MW	Steam Turbines (ST)	Once Through
Central Energy Facility	Central Electric Power	Natural Gas	7.2 MW	Gas Turbines (GT)	Cooling not required
City of Seneca	City of Seneca	Petroleum (DFO)	9 MW	Internal Combustion (IC)	Cooling not required
Valenite	Central electric power	Petroleum (DFO)	2.4 MW	Internal Combustion (IC)	Cooling not required
John S Rainey	SC Public Service Authority	Natural Gas	977 MW	Combined cycle (CA/GT/CT)	Once Through Recirculati ng
Urquhart till 2013	SC Electric and Gas Company	Coal and Natural Gas	250 MW	Generic Combined cycle-GT/ST/CT	Once Through
Urquhart from 2013	SC Electric and Gas Company	Natural Gas and DFO	640 MW	Combined cycle-GT/ST/CT	Once Through
Savannah River Site Biomass Facility	AMERESCO	Bio-Power Wood derived substrate(WDS) and DFO	16 MW	Steam Turbine (ST)	Once Through

[9] Source: Form EIA-923, Union of Concerned Scientists. 2012. UCS EW3 Energy-Water Database V.1.3. www.ucsusa.org/ew3database and EIA State Profile and Energy Estimates, https://www.eia.gov/state/?sid=SC

[10] A power plant represents an electricity producing site and the aggregation of components all the way from the fuel input to the electrical output with one or more electrical generating unit (EGU) that each have a specific turbine structure.

Jasper	SC Electric and Gas Company	Natural Gas and DFO	862 MW	Combined cycle -CA/CT	Once Through
J Strom Thurmond	USCE-Savannah	Water	336 MW	Hydraulic Turbine	N/A
Jocassee	Duke Energy Carolinas LLC	Water	780 MW	Hydraulic Turbine – Pumped Storage	N/A
Keowee	Duke Energy Carolinas LLC	Water	152 MW	Hydraulic Turbine	N/A
Bad Creek	Duke Energy Carolinas LLC	Water	1,360 MW	Hydraulic Turbine-Pumped Storage	N/A
Rocky River	City of Abbeville	Water	3.6 MW	Hydraulic Turbine	N/A

Figure 2-1: Estimated water withdrawals in the US, by category in 2010.[11]



[11] Maupin, M. A., Kenny, J. F., Hutson, S. S., Lovelace, J. K., Barber, N. L., & and Linsey, K. S. (2014). *Estimated use of water in the united states in 2010.* (No. Circular 1405, 56 p.,). U.S. Geological Survey. Retrieved from http://dx.doi.org/10.3133/cir1405.

Figure 2-2**:** Map of electricity producing facilities in the Savannah Basin, South Carolina.

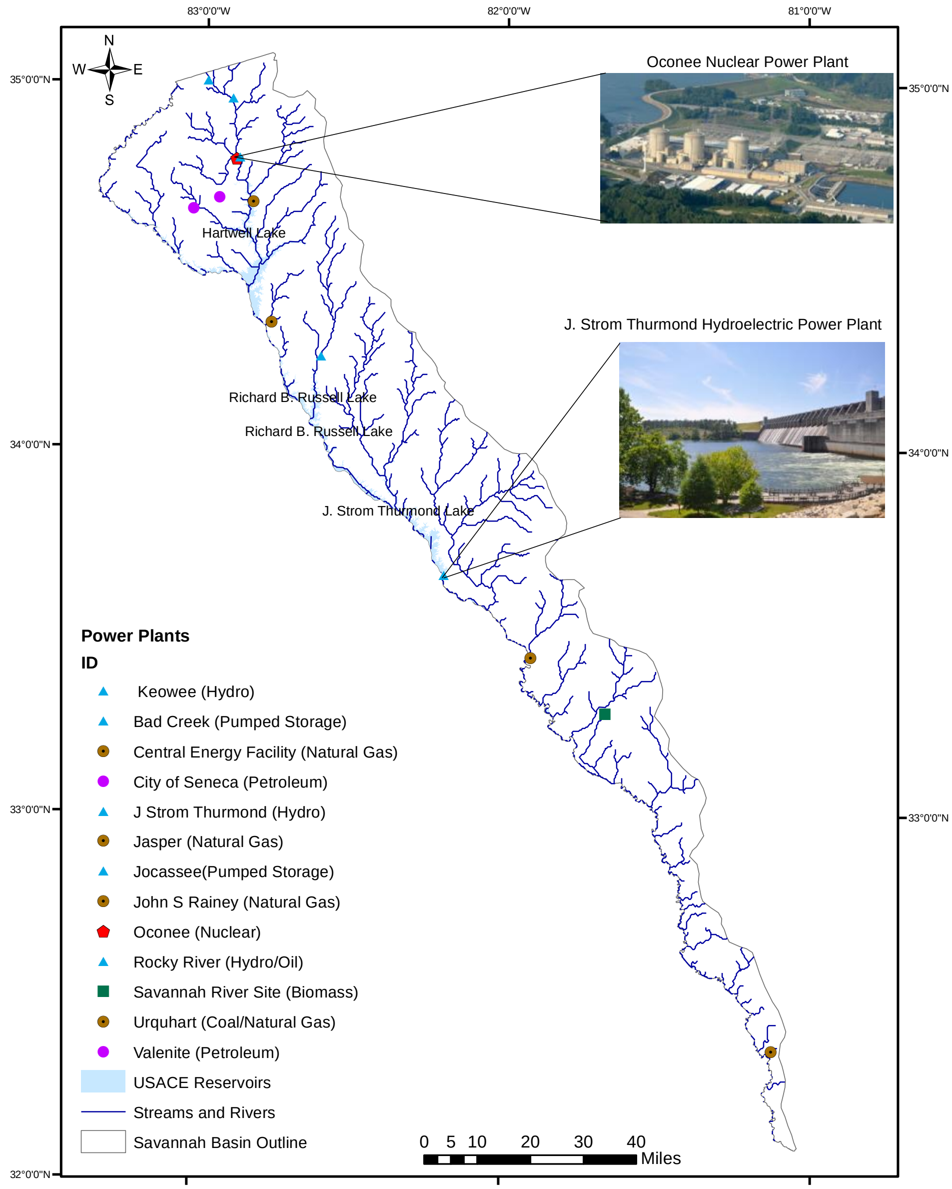


Figure 2-3: Net electricity generation from 1950 with future predictions till 2035 along with total water use in electricity sector in the US. Note the different scales between the right and left axis.

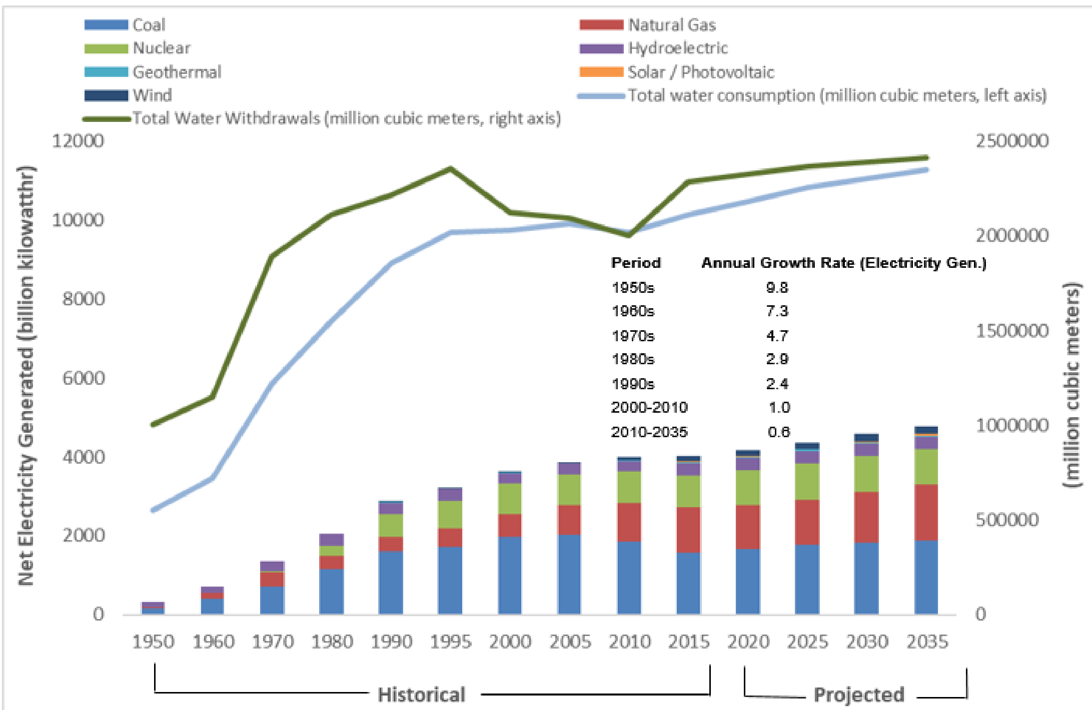
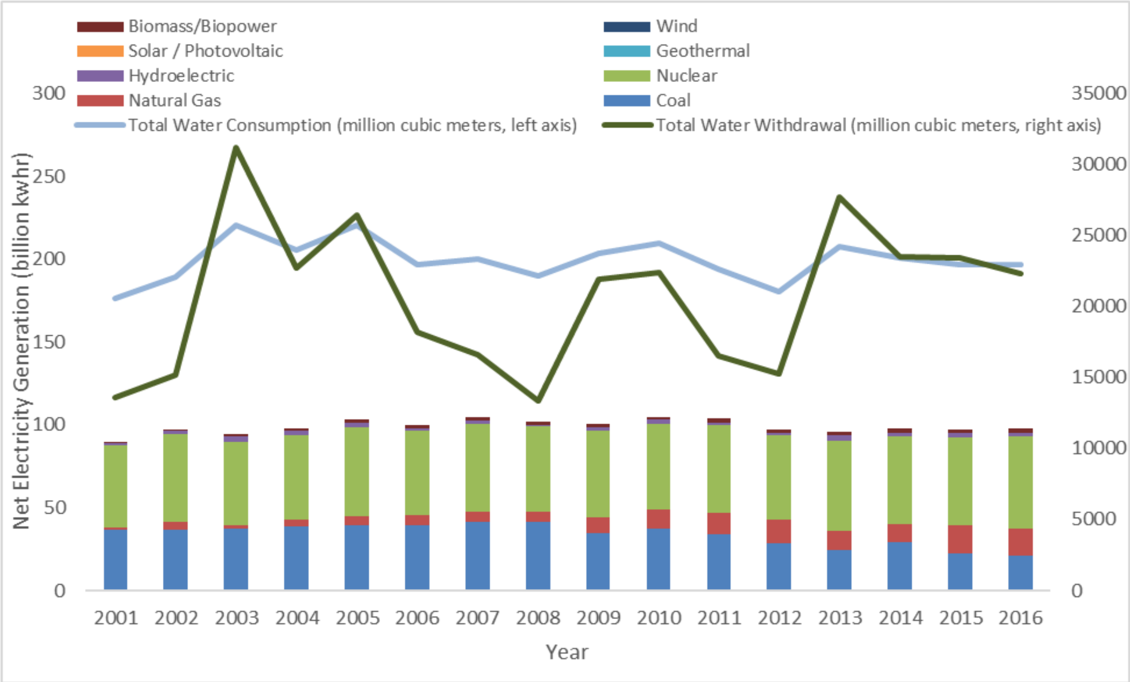
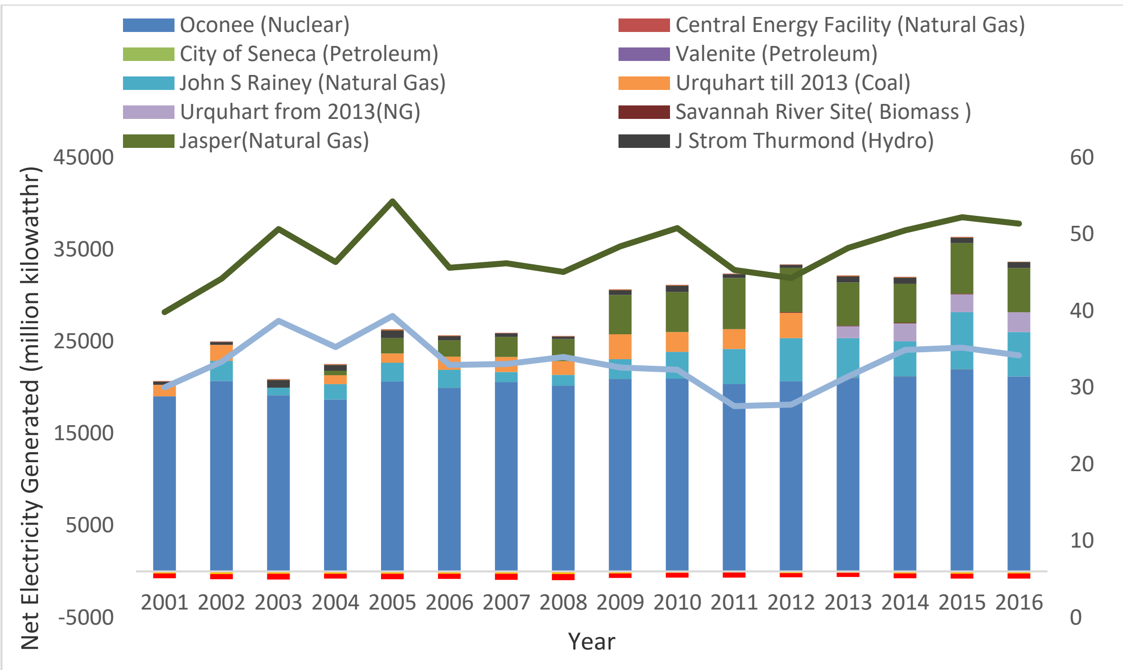


Figure 2-4: Net electricity generation[12] from 2001 till 2016 along with total water use in electricity sector in South Carolina. Note the different scales between the right and left axis.



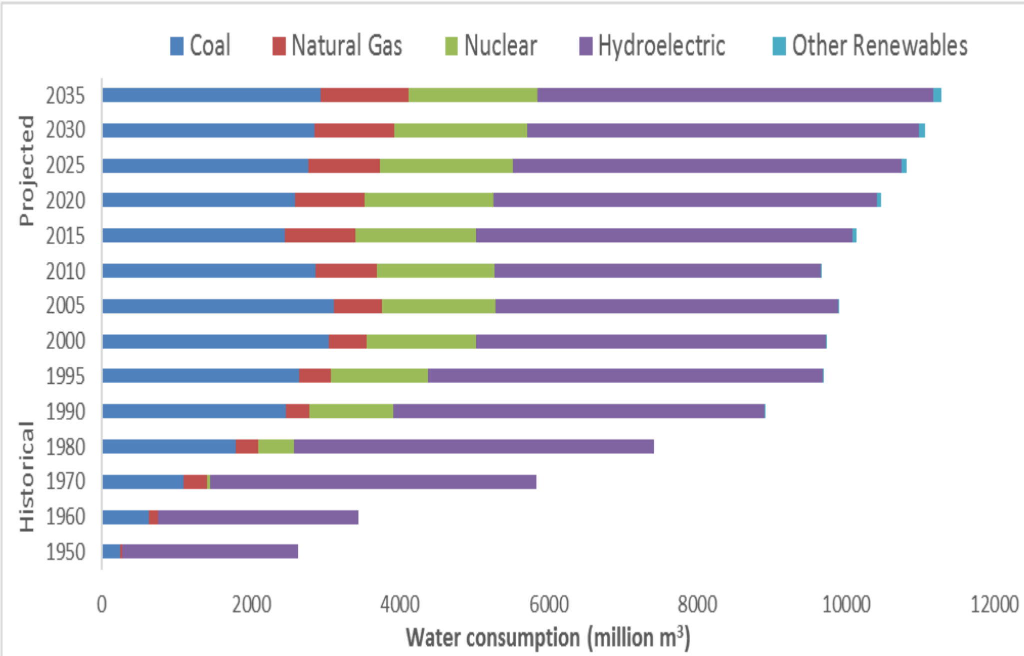
[12] https://www.eia.gov/state/analysis.php?sid=SC and EIA AEO2012, www.eia.gov/outlooks/archive/ae012/

Figure 2-5: Net electricity generation[13] from 2001 till 2016 along with total water use in electricity sector in Savannah River Basin.



[13] EIA AEO2012, www.eia.gov/outlooks/archive/ae012/

Figure 2-6: Annual water consumption and withdrawal/manipulation by different electricity generating sources from 1950 till 2035.



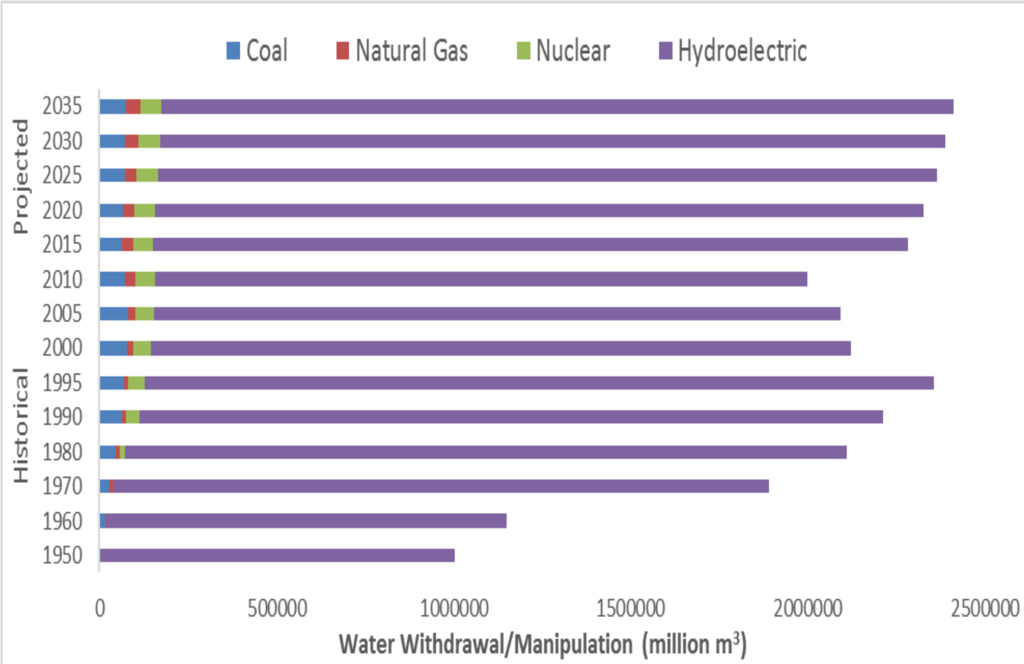


Figure 2-7: Annual water consumption and withdrawals/manipulation by different electricity generating sources in South Carolina from 2001 till 2016.

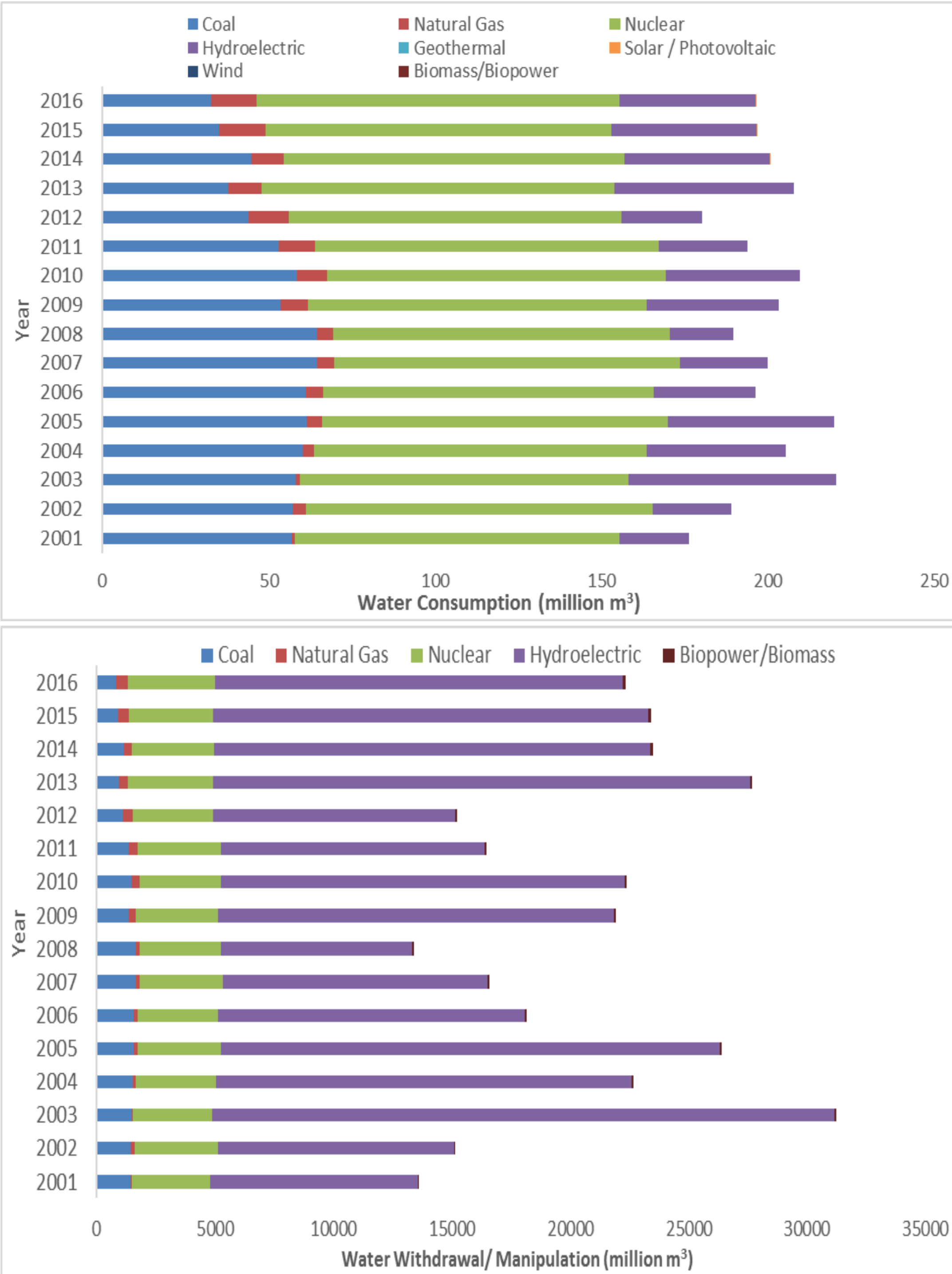


Figure 2-8: Water consumed by electricity generating units within the Savannah River Basin.

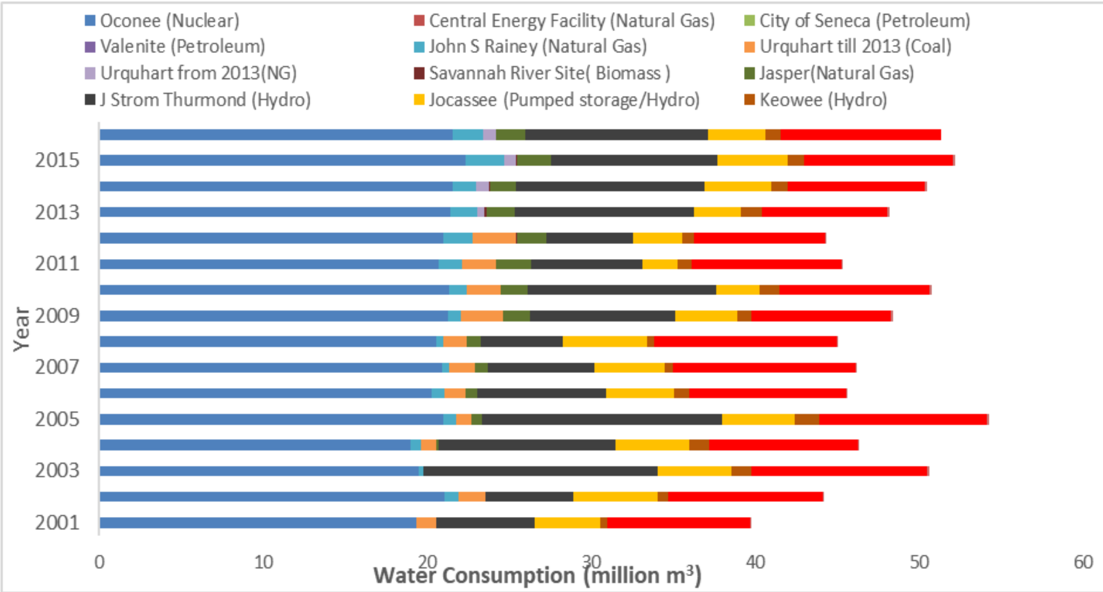
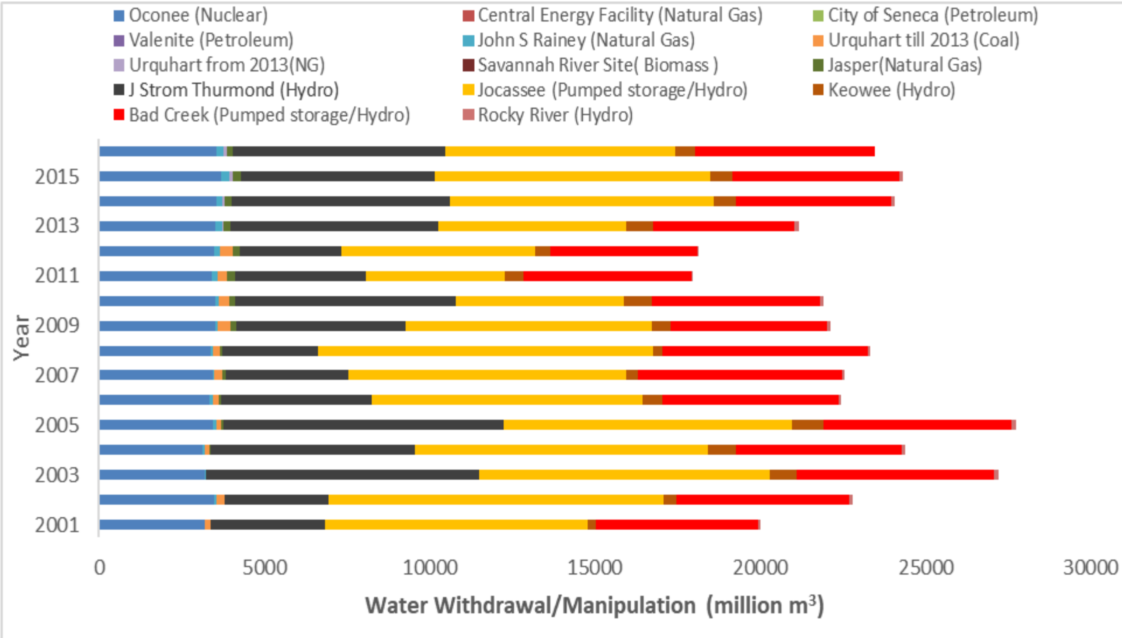


Figure 2-9: Water withdrawn/manipulated by electricity generating units within the Savannah River Basin



CHAPTER THREE

LOCAL AND LANDSCAPE FACTORS INFLUENCE OCCUPANCY OF FRESHWATER MUSSELS IN THE SAVANNAH RIVER BASIN, SOUTH CAROLINA

ABSTRACT

The two well-known consequences of water resource appropriation by electricity production are habitat degradation and fragmentation; which have caused a significant decline in freshwater mussels since the last decade. The Savannah river basin in South Carolina is known for its diverse mussel fauna and is home to the endangered mussel Carolina heelsplitter (*Lasmigona decorata*). We used an occupancy modeling approach to estimate the presence of 11 mussel species at 15 locations in the Savannah River Basin and to evaluate the local habitat and landscape factors that drive the distribution of rare and common mussel species in this basin. *Elliptio spp*. complex was the most abundant taxon and occurred at 45% of the sites. The endangered *Lasmigona decorata* was found at only 20% of the sites. Among species, estimated detection probabilities ranged from 0.27 to 1.0, whereas the estimated occupancy probabilities ranged from to 0.14 to 0.53. We fitted local and landscape level covariates to occupancy models and sampling covariates to detection models. Detection was primarily influenced by average stream depth, air and water temperature and occupancy was found to be governed by average stream width, substrate heterogeneity, conductivity, dam density and distance from major and small dams. We conclude that a combination of local and landscape level factors influence the occurrence of freshwater mussels in the Savannah river basin. Our findings show the need for conservation actions aimed at preventing loss of stream microhabitat due to degradation and fragmentation caused by the presence of dams and surrounding land use and augmenting the available freshwater mussel populations.

Keywords: Freshwater mussels, Occupancy, endangered species, Akaike's Information Criterion (AIC), multimodel inference

INTRODUCTION

The Southeast United States has abundant freshwater resources supporting a rich aquatic biodiversity and high species diversity of freshwater mussels which has been experiencing drastic decline since the past decades (Burch, 1973; Neves, Bogan, Williams, Ahlstedt, & Hartfield, 1997). This region is also an emerging economy based on tourism, agriculture, industry and power generation (Gleick, 2003; Sun, McNulty, Moore Myers, & Cohen, 2008). Recent studies have highlighted concerns about stress on the regional and local water resources in counties of the south-eastern states due to global climate change and rapidly growing economies (U.S. General Accounting Office, 2003) . These factors are bound to strain the region's water resources and are likely to have detrimental effects on the region's unique aquatic biota (Haag & Williams, 2013; Neves et al., 1997; Williams, Warren Jr, Cummings, Harris, & Neves, 1993).

Freshwater mussels have earned the moniker "ecosystem engineers" for the role they play in influencing the physical, chemical and biological processes within their aquatic habitat. They are known to stabilize the sediment, improve water quality and clarity by removing phytoplankton, bacteria and heavy metals, deposit filtered organic material that acts as a food source for aquatic invertebrates and fish, and provide a key food source for muskrats, racoons and even some salamanders (Haag & Williams, 2013; Strayer et al., 2004; Vaughn, 2010). Thus, freshwater mussels serve as indicators of ecosystem health because of their extensive connections to a large number of community- and ecosystem-level processes. Freshwater mussels belonging to family Unionidae are widely distributed in North America with 297 recognized taxa. Of these only 70 are currently stable and several are classified as Extinct, Endangered or Threatened (Neves et al., 1997; Williams et al., 1993). The southeast is a freshwater mussel biodiversity hotspot harboring approximately 250 species (Lydeard & Mayden, 1995; Williams et al., 1993). The Savannah River Basin, a major drainage of the Southern Atlantic Slope basin harbors 21 native freshwater mussel species including a few critically imperiled and high priority species. The precipitous decline in mussel populations has been attributed to habitat loss (Arbuckle & Downing, 2002; Gagnon, Michener, Freeman, & Box, 2006), impoundments (Allen, Galbraith, Vaughn, & Spooner, 2013; Galbraith & Vaughn, 2011; Vaughn & Taylor, 1999), change in land use (BrimBox & Mossa, 1999; Shea, Peterson, Conroy, & Wisniewski, 2013), pollution (Gangloff, Siefferman, Seesock, & Webber, 2009) and spread of invasive species (Haag & Williams, 2013; Vaughn & Spooner, 2006; Williams et al., 1993).

The ecological and geographic factors that drive the distribution of mussels are poorly understood (Strayer & Fetterman, 1999), which magnifies the difficulty of management in the context of conservation threats. Brim Box et al 2002 summarized three factors affecting distribution of mussels; presence and compatibility of host fish (Haag & Warren, 1998), micro habitat requirements (Layzer & Madison, 1995; Strayer & Ralley, 1993; Wisniewski, Rankin, Weiler, Strickland, & Chandler, 2014) and landscape-driven catchment scale factors (Baldigo, Riva-Murray, & Schuler, 2004; McRae, D Allan, & Burch, 2004; Shea et al., 2013). Studies on microhabitat factors such as stream current velocity, substrate composition and stability, water depth and water quality parameters such as DO, pH, conductivity have received considerable support in the past (Strayer & Ralley, 1993; Vaughn, 1997). On the other hand, a few studies advocate the importance of complex hydraulic characteristics such as shear stress, Froude number, Reynolds number (Re) measured over high- and base flows over simple hydraulic variables and that these microhabitat factors may not be as effective in predicting mussel occurrences in most cases (Layzer & Madison, 1995; Gangloff & Feminella, 2007). Recent studies specifically focusing on landscape driven catchment scale factors incorporating the effect of surface geology, soils, hydrologic alteration and land use associated disturbances have successfully predicted mussel occurrences (Baldigo et al., 2004; McRae et al., 2004; Pandolfo et al., 2016; Peterson, Wisniewski, Shea, & Jackson, 2011; Shea et al., 2013) in many southeastern rivers. In case of the Savannah Basin, the combined effect of impoundments and aberrant change in land use appear to have modified the ambient micro and macro habitat requirements of native mussels by altering the natural flow regimes, changing the thermal regimen and magnitude, frequency and duration of the hydraulic flows and transforming the substrate having serious repercussions on freshwater mussel populations (Alderman, 1998; Lytle & Poff, 2004; Savidge, 2007; SCDNR, 2015; SCDHEC, 2010; SCDNR, 2003).

The key step towards protecting mussel species in the Savannah Basin is to identify the important environmental factors influencing occurrence of mussel species and utilizing this information to implement effective conservation and management strategies. While the mainstem Savannah River in South Carolina is known to support a variety of mussel species (Keferl, 1993; Savidge, 2007), many of the tributary streams and creeks have not been surveyed for native mussels both historically and in the present. The aim of this paper is to identify local- and watershed-level landscape factors that influence the occurrence of the freshwater mussel populations in the Savannah River Basin. The objectives are to establish the distribution of endangered and threatened freshwater mussel species in the small order streams and evaluate the influence of local and landscape variables on the distribution of all encountered mussel species in the Savannah River Basin.

METHODS

Study Area

We conducted our study on 15 streams in the Savannah Basin in South Carolina (Figure 3-1). The Savannah River defines the state boundary between Georgia and South Carolina and the river basin is shared with North and South Carolina. In South Carolina, the river basin encompasses three physiographic regions: The Blue Ridge Province where the headwaters originate, and the Piedmont and Coastal Plain Provinces where majority of the river's drainage basin lies. Our study focusses on assessing the freshwater mussel distribution within the Savannah-Piedmont ecobasin which encompasses 36 watersheds and protected areas which form the Sumter National Forest. Land cover in the basin is dominated by forest cover, followed by cultivated land and more recent urban developments. It also contains 143 square miles of impoundments, namely reservoirs Hartwell, Richard B. Russell and J. Strom Thurmond/Clarks Hill built by US. Army Corps of Engineers, which retain most of the upstream available water of the mainstem Savannah River. The tributaries in the Savannah Piedmont ecobasin have not been extensively surveyed before for the presence of rare and endangered mussel species (Britton, Fuller, Smith, & Brisbin, 1979; Savidge, 2007).

The sampled streams are wadable (Strahler stream order 1 to 3). Streams such as Golden Creek, Wolf Creek, Eighteen Mile Creek, Rocky fork and Ramsey Creek in the inner piedmont region at the foothills of Blue Ridge typically have moderate gradients with moderately turbid water, mostly runs and riffles interspersed with pools and substrate includes a combination of detritus, sand, gravel and cobble, with infrequent boulders and exposed bedrock (Kohlsaat, Quattro, & Rinehart, 2005). The other ten surveyed streams were in outer piedmont region having less gradient and more flowing pools than swiftwaters. Substrate is mostly heterogeneous with cobble and boulders to slate bedrock and silt, sand and woody debris (Kohlsaat et al., 2005). More recently, due to poorly planned land use conversion and highly erodible soils these streams are subject to heavy siltation.

Mussel Sampling

We surveyed 15 sites for freshwater mussels between 2014 and 2016, following the protocol for sampling freshwater mussels in wadable streams by Wisconsin Department of Natural Resources (Piette, 2005). The sample streams represented a range of reach-scale habitat and riparian land use. The sites were at least 2 km apart and were selected using a combination of randomized sampling technique (Strayer & Smith, 2003) and preference based on the occurrence of endangered and threatened species from previous documented surveys. Based on prior mussel surveys in the Savannah Basin, the upper piedmont ecobasin region has no records of any native freshwater mussel presence. We randomly selected the sites from the upper piedmont region based on the South Carolina Stream Assessment (SCSA) from 2006 to 2011 which assessed nearly 500 wadable streams. The sites from the outer piedmont region had previous records of native mussel species presence and were chosen based on the presence of threatened or endangered species at those sites (Alderman, 1998; Bogan & Alderman, 2008; Keferl, 1993; USFWS, 2002). The sampling duration was chosen to avoid interfering with the spawning of the long-term brooding (bradytictia) and short-term brooding (tachytictia) mussel species. As mussels are sedentary organisms, we assumed the survey sites to be closed to changes in occupancy (MacKenzie et al., 2002; Piette, 2005). We conducted presence/absence surveys to establish species lists of mussels present at each of the 15 sites surveyed (Table 3-1). From

2014 to 2016, four surveys (one in 2014, two surveys in 2015 and one in 2016) were conducted at the 15 sites between May to September. The reason for spreading the surveys apart was that several sites were potential habitat for the endangered Carolina heelsplitter and repeat visual and tactile surveys within a short duration of time could potentially disturb the substrate and prove detrimental to the survival and recruitment of this species. The survey order was randomized among the sites. During each survey, observers searched for mussels along both banks for a total of one hour. If mussels were found the search was extended to a maximum distance of 200 m for streams < 15 m MSW and for two hours (4 man-hours) (Piette, 2005). We traversed along the stretch of the wadable stream and used visual/tactile method of surveying using a bathyscope to search for mussels. When a mussel was encountered, it was identified and anterior-posteriorly photographed and returned to the mussel bed after all sampling was completed. For endangered and threatened species, when found thorough pictures were taken and GPS location was recorded before returning them back to the sediment bed.

Covariate Measurements

To model variability in detection probabilities, we recorded Julian Day, searcher experience, air and water temperature (°C) and mean depth (cm) at each site during each survey. Ten measurements of stream depth throughout the site were taken at different points to incorporate the variation of pools, riffles, and runs.

The covariates to model variability in occupancy of mussels were divided into two levels, local- and landscape-level covariates. Substrate composition (modified Wentworth scale), substrate heterogeneity, dominant macrohabitat (%swift waters / %slack waters), specific conductivity (µS) and mean stream width (m) were visually estimated and recorded for each site at the local scale. The substrate categories included % detritus, % sand/silt/clay, % gravel, % boulder, % bedrock and substrate heterogeneity was determined using Shannon diversity index.

We obtained landscape covariates using ArcGIS 10.5 (ESRI, 2016). All map layers were projected in the State-Plane South Carolina FIPS 3900 North American 1983 Datum. To best assess the significance of landscape factors in driving occupancy of freshwater mussels the landscape structure was quantified at two spatial scales. The 'site' scale with a 600-m circular radius centered on the sample sites and the 'watershed' scale includes the HUC10 watershed (1:24,000) in which the sampling unit occurred. Land cover data was obtained from USGS Gap Analysis Project (USGS GAP, ESRI) spatial data describing vegetation and land use at (https://gapanalysis.usgs.gov/gaplandcover), and the Spatial Analyst Extension for ArcMap 10.5 was used to calculate areal percentages of forest, agricultural and urban land use for each site at two spatial scales. The county road map by the US Census Bureau (https://www.census.gov/cgi-bin/geo/shapefiles/index.php?year=2016&layergroup=Road) along with the Spatial Analyst Extension for ArcMap 10.5 were used to determine the road density (meters/sq.meters) at the two spatial scales. The dam density (dams per meter of stream length in HUC 10 watershed) was determined at the catchment scale. The distance in meters to a major dam (⩾15 m in height) (Source: National Inventory of Dams and National Hydropower Plant Dataset, ORNL) and small dam (mill/pond dam) (Source:

State permitted small dams, SCDNR) was calculated as the along the stream distance/dendritic distance between each sampling location and the nearest major and small dam respectively using the Network Analyst Tool in Arc Map 10.5 (ESRI, 2016). All raster files were set to the same spatial extent and were analyzed within a 30 × 30 m grid size. Finally, all the 15 sites were classified based on management activity at sites (United States Forest Service Land v/s Non-USFS). The habitat type is described using a binary-dummy covariate, with each site being either USFS Habitat (1) or N-USFS Habitat (0). All the covariates were **s**tandardized by converting raw data to a z score (subtracting the mean and dividing by the standard deviation for each covariate). We also conducted multivariate correlation analysis using JMP PRO 12 (SAS Institute Inc.,) and all highly correlated covariates ($r > 0.60$) were not included in the same model.

Data Analysis

Occupancy models use a multinomial maximum likelihood approach to evaluate information from repeated site visits (k=4, n=15) to estimate ψ, which is the probability that a site is occupied, as well as p_i (the probability of detecting the species on survey i, given the species is present on the site (MacKenzie et al., 2002). The occupancy parameter ψ_i is expressed as a logit function of site-specific local and landscape covariates (Table 3-2) and detection probability p_i is expressed as a logit function of sampling covariates (Table 3-2). Single Season occupancy models come with these main assumptions that 1) sites are closed during sampling, 2) sites are independent of one another 3) probability of occupancy and detection is equal across all sites any heterogeneity is attributed to the respective covariates and 4) the species is not misidentified i.e. there are no false positives (MacKenzie et al., 2006). Assumptions 1 and 2 were met for our study as all the sites were located far apart and the sampling at each site was completed within 2 to 4 hours. Freshwater mussels are sedentary organisms, it is highly unlikely that the assumption of the site being closed was violated. The sites were physio-geographically different and located in different watersheds, hence assumption 3 was not met at some sites. This variation in between sites was accounted for by the selection of habitat covariates at multiple spatial scales. Moreover, to avoid misidentification errors, the highly similar species *Elliptio complanata, Elliptio icterina, Elliptio producta* and *Elliptio angustata* were pooled together to form the *Elliptio spp. complex* for our analysis.

We ran single-species single-season occupancy models incorporating environmental covariates to reduce variance in parameter estimates while accounting for imperfect detection using Program PRESENCE 11.8 (Hines, 2006) available for download from http://www.proteus.co.nz/). These models were run for all freshwater mussel species that had adequate detections to fit an occupancy model. We used a two-step process to estimate occupancy (Bailey, Simons, & Pollock, 2004; Kroll et al., 2008). First, we ran detection only models where importance of each sampling covariate was tested, ψ(.) *p* (sampling covariates). In the second step, occupancy models with local-level only covariates [ψ(local) *p* (best model)] and landscape-level only covariates [ψ(site/watershed) *p* (best model)] were analyzed with the best model for detection probability (MacKenzie et al., 2006). Covariates appearing in models with $\Delta AIC_c < 4$ were retained for a final candidate model set that included a combination of local and landscape (site and catchment) level factors.

The models were selected and ranked based on Akaike's Information-theoretic Criterion for small sample sizes (AIC_c) (Burnham & Anderson, 2002). The difficulty in choosing a single best approximating model is not a defect of AIC or any other selection criterion but instead points to the insufficiency of data to explain occupancy patterns. A multimodel inference is useful for providing robust inference when a candidate model set has multiple top-ranking models (Burnham & Anderson, 2002). We ran the Goodness of fit test on the global models for each species with 10,000 bootstrap samples to obtain the over dispersion or variance inflation factor $\hat{c}$. Global models having $\hat{c} > 1$ indicated over dispersion of data resulting in the need to replace AICc with Quasi AICc ($QAIC_c$) and parameter standard errors need to be inflated (Burnham & Anderson, 2002; McCullagh & Nelder, 1989). The global models for 4 out of 8 freshwater mussel species had the $\hat{c} > 1$, hence model selection was done based on $QAIC_c$. The models were ranked using the AICc or QAICc and their weights ($AIC_{c\ w}$ or $QAIC_{c\ w}$) which range from zero to one with the best approximating model having the highest weight of one. The top candidate model set contained all models with a ΔAIC_c or $\Delta QAIC_c < 4$ which offer substantial support (Burnham & Anderson, 2002). The summed model weights were obtained for each occupancy covariate to by summing the Akaike weights ($AIC_{c\ w}$) for all models in which the occupancy covariate was used to determine the relative importance of the said covariate in the candidate set of models (Anderson, Burnham, & White, 1998; Burnham & Anderson, 2002). Due to small sample size and low detections, for some models the numerical convergence was not reached or warning about the variance-covariance matrix indicating untrustworthy SE's was obtained. In such situation, the models were deleted from the top-ranking model set, replaced by the next best model. However, the top models selected do not necessarily represent all the environmental or habitat covariates that influence the detection and occupancy of mussels in the study area (MacKenzie & Bailey, 2004). To account for model and parameter uncertainty, we calculated model-averaged site occupancy estimates for each species based on the top models (ΔAIC_c or $\Delta QAIC_c < 4$) in the candidate set (Table 3-4).

RESULTS

Distribution

Of at least 25 freshwater mussel species described within the Savannah basin (Savidge, 2007) and 15 species known to occur in the Savannah Piedmont ecobasin, eleven species belonging to eight genera were collected across the 15 sites (Table 3-1) with observed site richness ranging from 0- 11 (mean ~5). One species is federally endangered (*Lasmigona decorata*), two are listed as threatened by South Carolina's Priority Species List (*Alasmidonta varicosa* and *Lampsilis cariosa*) and other four species are not known to be of conservation concern in the basin. We did not encounter any freshwater mussels in seven of the 15 sampled sites. Of the eight occupied sites, five sites where a maximum number of species were encountered occurred in the Turkey Creek watershed which is a critical habitat for the federally endangered, *L. decorata* and state threatened *A. varicosa* and *La. cariosa* (Kohlsaat et al., 2005; Trainor & Carr, 2005; USFWS, 2012). One site occurred in the Little River-Savannah River watershed and 2 sites occurred in the Long

Cane watershed which lies within Long Cane Ranger District of Sumter National Forest. Altogether, the most dominant species during the survey was *Elliptio complanata* which was observed at 8 of the 15 sites and had a naïve occupancy of 0.5. Due to difficulty in taxonomic identification of species belonging to genus *Elliptio*, we pooled *E. complanata*, *E. producta*, *E. angustata* and *E. icterina* into *Elliptio spp. complex* for the occupancy models. The rarer species were *A. varicosa* and *La. cariosa* which was observed at only 2 sites, with a naïve occupancy of 0.13.

Factors Influencing Species Detection and Occupancy

We obtained average detection estimates for all species from the null models of the respective species. The mean detection estimates among species ranged from 0.27 to 1.00. The 95%CI associated with the detections probabilities for all mussel species did not include 0 and hence these estimates were considered precise (Table 3-3). We assessed five sampling covariates for detection probability, including the null and global model. The top detection model varied among species. All species except two had top detection models with covariates suggesting that environmental factors may affect detection of the species. For *Elliptio spp.* complex and *Strophitus undulatus*, the top model was a null model with constant detection indicating no need to correct for detection bias. For *A. varicosa*, *La. cariosa*, *Uniomerus carolinianus* and *Villosa delumbis*, the detection probabilities were positively influenced by average stream depth (cm), and for *Pyganodon cataracta* and *L. decorata* the detection probabilities were positively influenced by air temperature (°C) and water temperature(°C) respectively (Table 3-4).

Estimates of occupancy varied across species and sites (Figure 3-2). The estimated occupancy probabilities among species ranged from 0.14 (0.034 - 0.41) for *A. varicosa* to 0.53 (0.30 - 0.76) for *Elliptio spp.* complex (Table 3-3). All occupancy estimates were considered precise (95% CI's did not include 0; Table 3-3). The estimated occupancy was identical to naïve occupancy for only one species, *Elliptio spp.* complex. The estimated occupancy for remaining seven species was slightly higher the naïve occupancy, which however was associated with high standard errors, suggesting these estimates were biased by low detection probability across sites for these species.

The intercept only null model, Ψ (.), *p*(.) was the best ranked model for five species, *A. varicosa, La. cariosa, U. carolinianus, P. cataracta and L. varicosa*. The global models for these species indicated overdispersion of data (Table 3-4). $QAIC_c$ was used for model selection which favors models with fewer parameters thus leading the null model (K=2) to be the best ranked model. All species had at least one environmental covariate influence site occupancy. Site-scale landscape covariates featured as a top model for only one species, *La. cariosa.* On the other hand, the landscape-scale site or watershed level covariates were included in the top models (ΔAIC_c or $\Delta QAIC_c < 4$) of all species except *A. varicosa***.** However, watershed-level landscape covariate was ranked the best approximated model from the candidate set only for one species, *S. undulatus.* Local habitat covariates featured in top models (ΔAIC_c or $\Delta QAIC_c < 4$) for all species expect *La. cariosa* and were ranked the best model for *Elliptio spp.* complex and *V. delumbis*. The model averaged occupancy estimates based on top-ranked models are comparatively higher that naïve occupancy estimates, indicating the importance of the environmental (local and watershed) variables in predicting site-occupancy (Table 3-4). Finally, the top models included in our candidate sets for the eight species do not necessarily represent all the environmental or habitat covariates that influence the detection and occupancy of the freshwater mussels in the study area.

Average stream width (m), a local-scale stream habitat covariate, best explained occupancy in six of the eight encountered freshwater mussel species (Figure 3-3 shows a positive association to average stream width though the 95% confidence intervals around β_i overlapped with zero). In *Elliptio spp.* complex, average stream width along with % swiftwaters was the top model, with occupancy increasing with average stream width (m) and % swiftwater (Table 3-4; Figure 3-3). Substrate Heterogeneity appears to be the second most influential local habitat covariate having a positive effect on site occupancy of *Elliptio spp. complex, P. cataracta, S. undulatus* and *L. decorata.* Conductivity as a local habitat covariate was positively associated with site occupancy for *Elliptio spp.* complex and *V. delumbis*. However, the 95% CI's around the β_i's for the all local-scale habitat covariates featuring in top models for the eight-species included zero and hence their effect on site occupancy of the eight species is unclear due to wide confidence intervals around the estimates.

Amongst landscape covariates, the effect of presence of dam seems to influence occupancy of several encountered species. While models for several species included dam density as a covariate, the error estimates in most cases suggested no strong influence of dams on occupancy. *Ellitio spp.* and *V. delumbis* were exceptions to this trend, as the model coefficients indicated a significant negative influence of dams on the occupancy of these species. The distance to major dam (m) had a surprising conclusive negative effect on site occupancy for only one species, *U. carolinianus* (95% CI around βi did not include zero; Table 3-4). For *S. undulatus* and *L. decorata*, the 95% confidence interval around the covariate distance to small dam (m) included zero suggesting no strong influence of proximity to small dams. Another important landscape covariate, presence of forested area had a positive effect on site occupancy of *La. cariosa* (Table 3-4). The binary coded landscape variable of habitat was second best model ranked in the candidate set for *La. cariosa*. Sites within US Forest Service land (protected land) had double the site occupancy probability compared to sites not within the US Forest Service land (Figure 3-3-h; Table 3-4).

Summed weights help identify the importance of a variable by making inference from the top models within candidate set for each species (Burnham & Anderson, 2002). For *Elliptio spp.* complex, the summed model weights for each occupancy covariate were, average width= 0.60, substrate heterogeneity= 0.37, dam density= 0.10 and conductivity= 0.08 (Table 3-4). Average stream width appears to be the most important factor driving site occupancy for *Elliptio spp.* complex. Only two models were included in the top candidate model set for *A. varicosa* with the null model and local habitat covariate average stream width (m) having a summed weight of 0.15 (Table 3-4). It appears that average stream width (m) only poorly predicts site occupancy for this species with no other covariate being associated with its occurrence. *La. cariosa* was the only species to have all landscape level covariates along with the null model in the top candidate model set. The summed weights were habitat= 0.22, dam density= 0.21,

%forest within a 600-m buffer= 0.18 and % forest in HUC 10 watershed= 0.17. The species site occupancy is positively associated with forested area, with the covariates indicating a forested habitat having a summed weight of 0.58 (Table 3-4). The top candidate model set for *P. cataracta* included a null model followed by covariates associated with local habitat features and one landscape variable. The summed weights were average width = 0.20, substrate heterogeneity = 0.14 and dam density = 0.11(Table 3-4). In the case of *P. cataracta*, it appears that local habitat factors seem to positively drive site occupancy more that landscape level negative association with dam density, though all the parameter estimates were imprecise (95% CI included zero; Table 3-4). For *S. undulatus*, the top candidate set included two landscape level factors associated with dams, dam density and distance to small dam influencing site occupancy, with the summed weights of dam associated factors being 0.781 (Table 3-4) which indicates strong influence of presence of dams on site occupancy, although the null model was also the among the top candidate set, though all the parameter estimates were imprecise (95% CI included zero; Table 3-4). In case of *U. carolinianus* the null model appears in the top candidate model set along with average stream width (m) (summed weight= 0.18) and distance to major dam (miles) (summed weight= 0.10) (Table 3-4). Both these local and landscape level factors only offer weak support for site occupancy of Uniomerus. Site occupancy of *V. delumbis* was positively correlated to conductivity (summed weight= 0.46) and negatively related to dam density (summed weight= 0.4), with the parameter estimates of conductivity being imprecise and that of dam density being precise (Table 3-4). Lastly, for *L. decorata* four covariates along with a null model were a part of the top candidate model set. The summed weights of each occupancy covariate were local covariates average stream width = 0.24, substrate heterogeneity = 0.15, dam density = 0.11 and distance to small dams =0.05. All parameter estimates in the top model set for *L. decorata* were imprecise (95% CI included zero; Table 3-4).

DISCUSSION

Occupancy models have been used successfully to determine the influence of environmental variables on site-occupancy and sampling factors on detection while providing insight into the habitat and environmental factors influencing species distribution and abundance. Site occupancy has become an increasingly popular technique for examining distributions of freshwater mussel populations (Pandolfo et al., 2016; Shea et al., 2013; Wisniewski, Rankin, Weiler, Strickland, & Chandler, 2013). Because freshwater mussels are often difficult to sample due to their burrowing habits and sampling conditions, occupancy modeling provides a more accurate depictions of species' status and a better understanding of the factors that affect them (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003; Shea et al., 2013; Wisniewski et al., 2013; Wisniewski et al., 2014).

Impact of Heterogenous Detection and Factors Affecting Detection

We accounted for heterogeneous detection probabilities to avoid bias in our site occupancy estimates (MacKenzie et al., 2002; Pandolfo et al., 2016; Wisniewski et al., 2013). Variations in species detections are influenced by factors such as species' life history and biology, habitat associations, behavioral patterns, environmental conditions, sampling strategies and survey design (MacKenzie et al., 2002) as well as species density and abundance (Dorazio, Royle, Söderström, & Glimskär, 2006; Royle & Nichols, 2003). Variations in freshwater mussel detections have been attributed to several factors such as habitat (Meador, Peterson, & Wisniewski, 2011), burrowing behavior (Strayer & Smith, 2003; Wisniewski et al., 2013) and sampling and survey methods (Metcalfe-Smith, Di Maio, Staton, & Mackie, 2000; Shea et al., 2013; Wisniewski et al., 2013). We did not assess effects of other sampling techniques or designs on detection probabilities. Our study indicated that the estimated species-specific detection probabilities were < 1 for all species except *Elliptio spp.* complex and greatly varied among mussel species. We accounted of heterogeneity in detection probabilities by incorporating environmental factors such as water and air temperature, water depth, Julian day and observer. Species detections varied with average stream depth. Similar results are seen elsewhere where channel depth has been a popular predictor of mussel occurrence with detections increasing with depth (indicative of pool habitat) and has been positively correlated with abundance of *E. complanata* and on the other hand negatively correlated with abundance of *Alasmidonta undulata* (Baldigo et al., 2004; Strayer & Ralley, 1993; D. Strayer, Hunter, Smith, & Borg, 1994) . Detections for all species increased with observer experience. Experienced observers could be more successful at species detections due to ability to negotiate difficult sampling condition (Wisniewski et al., 2013) or being able to correctly identify similar looking species as misidentification is a common issue with freshwater mussel sampling. Per Royle and Nichols (2003), the probability of detecting a single individual of a species is proportional to the density of the given species. It appears that the low density and abundance may have resulted in heterogeneous detection probabilities in our study for all mussel species, except *Elliptio spp.* complex which had a detection probability of 1.0 throughout the sampling sites and *S. undulatus* who did not have any covariate effect on detection probability. The small sample size (N=15) accompanied with low proportion of area occupied, low rates of occurrence and rarity of species in the basin (except *Elliptio spp.* complex) could be responsible for low detection probabilities in our study (Dorazio et al., 2006; Roach & Barrett, 2015). Finally, erroneous site selection could bias rates of detection probabilities, though in case of our study it seems unusual as malacological experts from the area were consulted during the site selection process (Morgan Wolf, USFWS South Carolina Field Office, Pers. Comm)

Factors Affecting Occupancy

Freshwater mussels occurring in the streams of Savannah River basin do not occur in the usual form of high density mussel assemblages as previously reported from other regions (D. L. Strayer, 1993). Site-occupancy is generally related to mussel conservation status, with low occurrence for endangered and threatened species (Pandolfo et al., 2016). Even though mainstem Savannah River may have many endemic mussel species (Savidge, 2007), they seem to have disappeared from many streams and tributaries (Keferl, 1991; Keferl, 1993). We saw similar trend in our study. *Elliptio spp.* complex was the most dominant species in our study area (Table 3-3) and had occupancy estimates like other commonly found *Elliptio* species in the lower Flint river, Georgia (Wisniewski et al., 2013). The same goes for *V. delumbis* (Ψ = 0.47; Table 3-3) which has occupancy estimates consistent with those reported from a sister species *Villosa* *lienosa* ($\Psi = 0.40$) in the Lower Flint river, Georgia (Wisniewski et al., 2013). In terms of occupancy, *Elliptio spp.* complex and *V. delumbis* are consistent with their status as currently stable in South Carolina (Kohlsaat et al., 2005). *P. cataracta* and *U. carolinianus*, which are not of high conservation concern in the state, had relatively low occupancy probability among surveyed streams, which suggests a need for additional surveys to assess statewide status. *S. undulatus* was recently categorized as being species of highest priority in SCDNR's State Wildlife Action Plan (2015). *Lampsilis cariosa* and *Alasmidonta varicosa* are categorized as threatened species with the latter being included on a list of species being petitioned for consideration as candidates for federal protection (USFWS, 2011).

Influence of Local and Landscape-scale Environmental Factors

The emphasis of our study was to identify abiotic factors that influenced occupancy and distribution of freshwater mussels within the Savannah River Basin. The occupancy of all the encountered species was best explained by a combination of local and landscape-level factors indicating towards a likelihood that the landscape-level disturbances could be altering the local-scale microhabitat characteristics Traditionally several local microhabitat factors such depth, substrate type, current velocity, roughness and geomorphological variables such as shear stress have successfully predicted mussel occurrences albeit with weak associations (Baldigo et al., 2004; Gangloff & Feminella, 2007; Layzer & Madison, 1995; D. Strayer & Ralley, 1993). Based on our study, freshwater mussels were more likely to occupy sites with high average stream width (a surrogate for stream order). Smaller order streams have lower diversity and abundance of mussels as compared to higher order streams, probably due to difficulty in sustaining stream flow during high flows and susceptibility to fragmentation (Haag & Warren Jr, 2008). Freshwater mussel species are sensitive to the dominant substrate and substrate penetrability, with many species exhibiting marked differences in substrate preference. In our study, the site occupancy of mussel species increased with high substrate heterogeneity as mussels depend on stable substrates that can create flow refuges allowing mussels to filter feed steadily and consistently (Haag, 2012). Similar observations were noted in the Lower Flint River in Georgia, where *Elliptio sloatianus* prefers larger substrates such as gravel and bedrock and completely avoids clay substrate and on the other hand species such as *Elliptio fumata/pullata* and *Quadrula infucata* is found predominantly in clay (Wisniewski et al., 2014). Interestingly, throughout our study *L. decorata* occurred exclusively in sites with exposed slate bedrock outcroppings which is similar to the habitat requirements mentioned in the critical habitat reports for this endangered mussel species (USFWS, 2002).

In recent times, landscape factors such as hydrogeomorphology and land use have been more accurate at predicting mussel occurrences (McRae et al., 2004; Newton, Woolnough, & Strayer, 2008; Peterson et al., 2011; Shea et al., 2013). Our results suggest factors at a range of scales are more successful in accounting for the spatial variability in freshwater mussel site-occupancy when the assemblage is considered collectively. Our results identify the presence of dams which negatively affected site-occupancy for all species except *U. carolinianus* and presence of forested habitat which positively affected site occupancy as the most influential landscape-scale factors. Our results were consistent with previous studies that demonstrated the adverse effects of impoundments on freshwater mussel assemblages resulting in mussel stranding, reduced survival, recruitment and dispersal with imminent risk of extinction (Gangloff, Hartfield, Werneke, & Feminella, 2011; Peterson et al., 2011; Shea et al., 2013; Vaughn & Taylor, 1999). Small dams in lower order streams act as barriers to dispersal of potential host fish thereby preventing upstream colonization and distribution of these mussel species (Watters, 1996). Thus, based on our results, the combined effect of high dam density in the watershed and shorter distance to dams may restrict distribution of mussel populations causing them to become progressively isolated and thus susceptible to extinction. There are several examples of studies where mussel species occurrence was negatively influenced by the presence of impoundments (Galbraith & Vaughn, 2011; Gangloff et al., 2011; Vaughn & Taylor, 1999; Watters, 1999). Mill and pond dams on small streams act as barriers by preventing movement of potential host fish into upstream reaches and thereby interfering with the natural recolonization of unoccupied habitats causing reach isolation (Shea et al., 2013; Watters, 1999). The streams surrounded with high percent of forest cover would likely suggest a less altered stream hydrography with higher quality unaltered habitat when compared to sites outside of the protected habitats which might be under the influence of agricultural and urban land use which has adverse effects on survival and recruitment of mussel species by decreasing water quality and quantity, increasing sedimentation, altering stream flows and presence of host fish (Allan, 2004; Shea et al., 2013)

Our study also reflects a similar and well-known difficulty in obtaining precise parameter estimates and habitat associations of rare species. Even though our detection rates were moderately high (Table 3-3), most of the parameter estimates associated with local and landscape-scale covariates were accompanied with wide confidence intervals around the estimates due to high standard errors. We believe this may be because of small number of sites with detections (in case of rare species like, *L. decorata, A. varicosa and La. cariosa*) and small sample size in general. Hence, the results of our study should be interpreted with caution and a more exhaustive research to corroborate the habitat association of freshwater mussels must be conducted in our study area.

As expected, our results indicate that the richest mussel aggregations and occurrences were associated with sites with higher habitat quality, less fine substratum, overall higher substrate heterogeneity and lower specific conductance. Species diversity at a site was reflective of habitat complexity. The sites within the Turkey creek watershed and the Long Cane creek watershed contained diverse microhabitats of pools interspersed with swiftwater habitats and having a large proportion of cobble and boulder substrates with bedrock outcrops. These sites consistently exhibited higher species diversity and supported healthy freshwater mussel populations. In the Turkey creek watershed, we found populations of two S1 (critically endangered) species *L. decorata* and *A. varicosa* and two S2 (threatened within the state) species *La. cariosa* and *S. undulatus* in majority sampled reaches indicating this watershed provides refuge to numerous high conservation priority mussel taxa and should be the highest conservation target area within the Savannah river basin (Table 3-1). Similar habitat association have been reported from other studies within the Southern Atlantic Slope drainage where species such as *E. sloatianus, E. complanata, S. undulatus* and *A. varicosa* prefer swiftwater habitats, higher concentration of dissolved oxygen, higher percent boulder/gravel and lower percent sand/silt (Baldigo et al., 2004; Wisniewski et al., 2014). In terms of landscape-scale variables, the land use in the Turkey creek watershed is predominantly 81% forest cover, followed by 13% agriculture and 6% urban development; whereas the average land use within the three Upper Piedmont watersheds; Twelve-mile creek, Eighteen-mile creek and Chauga river is 53% forest cover with 34% agriculture and 11% urban/residential developments. High forest cover upstream of the sampled reaches as seen within the Turkey creek watershed would suggest an unaltered stream habitat with minimal flow alterations and sedimentation. Intensive agricultural and urban land use as seen within the upper-piedmont watersheds are indicative of decrease in water quality and quantity, increased siltation and influx of pollutants/nutrients into the streams and are likely to trigger decline in mussel populations and creating an extinction debt associated with habitat degradation (Poole & Downing, 2004; Shea et al., 2013). We do not have historical data on the distribution of freshwater mussels in the upper-piedmont region of the Savannah River Basin and hence we cannot firmly conclude if the above-mentioned sites were degraded habitats and hence could not sustain mussel populations.

CONCLUSION

The Southern Atlantic Slope Unionoid Faunal Province of North America is a unique freshwater mussel biodiversity hotspot (Lydeard & Mayden, 1995; Neves et al., 1997) and the Savannah river basin, a major drainage of the south atlantic slope harbors several endemic mussel species (Bogan & Alderman, 2008). The freshwater resources of the Savannah Basin are subject to high water usage especially during summer months to meet energy, agriculture and municipal needs courtesy of the expanding southeastern economy resulting in alterations to the natural flow of streams and rivers causing habitat fragmentation and degradation. It is vital that these waterbodies are preserved to ensure the long-term health of mussel populations within the Savannah River Basin. Our results support the claim that different freshwater mussel species respond to a variety of local and landscape factors having diverse management implications. Furthermore, our study substantiates the adverse effects presence of impoundments can have on the occurrence of highly-fragmented mussel populations especially the high priority species such as *L. decorata* and *A. varicosa*. The management and conservation practices in the Savannah river basin must therefore focus on conserving instream habitat in these small- order streams as well management of water quality and water quantity to establish by minimum flows across the spatial scales researched in this study. We also recommend construction of fish ladders and stream crossing in streams and tributaries that harbor endangered and threatened mussel species such as *L. decorata, A. varicosa* and *La. cariosa* to facilitate dispersal upstream of the impounding barriers. Trial on reintroductions of the endangered *L. decorata* in historically suitable habitats within the basin are underway to help resuscitate these species. E.g. a section of Flat Creek in Lancaster County, SC was stocked with 390 hatchery raised Carolina heelsplitters and a similar project is underway in a recently restored Gills creek in Lancaster County, SC (Morgan Wolf, USFWS South Carolina Field Office, Pers. Comm). Our results offer insights into the large- and small-scale habitat conditions that are likely to increase the probability of suitability habitat at reintroduction sites. In conclusion, extensive surveys of smaller order streams to establish distributional pattern along with continued qualitative and quantitative monitoring of these freshwater mussel populations will prevent their extirpation from the Savannah River basin.

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Table 3-1**:** Freshwater mussel species collected at the 15 sampling sites in the Piedmont Ecobasin of Savannah River Basin, South Carolina.

Species by Tribe[14]	**Common Name**	**Status (SC DNR, 2015)**[15]	**No. of Sites**
Pleurobemini			
Elliptio complanata (Lightfoot, 1786)	Eastern Elliptio	Currently Stable (S5)	8
Elliptio icterina (Conrad, 1834)	Variable Spike	Currently Stable (S4)	7
Elliptio producta (Conrad, 1836)	Atlantic Spike	Special Concern (S3)	5
Elliptio angustata (Lea, 1831)	Carolina Lance	Special Concern (S3)	4
Uniomerus carolinianus (Bosc,1801)	Eastern Pondhorn	Currently Stable (S3)	3
Lampsilini			
Lampsilis cariosa (Say, 1817)	Yellow Lampmussel	State Threatened (S2)	2
Villosa Delumbis (Conrad, 1834)	Eastern Creekshell	Stable/Species of concern (S4)	7
Anodontini			
Pyganodon cataracta (Say,1917)	Eastern Floater	Currently Stable (SNR)	3
Alasmidonta varicosa (Lamarck, 1819)	Brook Floater	State Threatened (S1 recomm.)	2
Strophitus undulatus (Say,1817)	Creeper (formerly, squawfoot)	Species of Special Concern (S2)	4
Lasmigona decorata (Lea,1852)	Carolina Heelsplitter	Federally and State listed Endangered (S1)	3
Total			**15**

[14] Burch, J. B. (1975). *Freshwater sphaerlacean clams, mollusca, pelecypoda, of north america* Malcological Publications.

[15] NatureServe: Status is assessed and documented at three distinct geographic scales-global (G), national (N), and state/province (S). S1 = Critically Imperiled, S2= Imperiled, S3= Vulnerable, S4= Apparently secure, S5= Secure

Table 3-2: Environmental covariates, type, mean values (min-max) and standard deviations (SD), included in candidate models to determine their effect on freshwater mussel occupancy in Savannah Basin, South Carolina.

Covariate	*Definition*	*Covariate Type*	*Mean (Min, Max)*	*SD*
OCCUPANCY:				
(.)	Occupancy assumed to be constant			
Local-scale				
Conductivity (µs/cm)	Varies with the mean conductivity measured using a Oaklon waterproof ECTestr™ 11	Continuous	115 (40, 250)	52.67
Average Width (m)	Varies with mean average width(meters)measured using a measuring tape	Continuous	7.38 (3.00, 13.50)	3.05
Substrate Heterogeneity	Varies with Substrate Heterogeneity calculated from measuring substrate type to nearest 5% at each site	Continuous	1.22 (0.61, 1.60)	0.33
% Swiftwater	Varies with amount of habitat classified as runs/riffles/ rapids to the nearest 5% at each site.	Continuous	52 (0, 90)	22.10
% Slackwater	Varies with amount of habitat classified as pools to the nearest 5% at each site	Continuous	48 (10, 100)	22.10
Landscape-Scale Site-level:				
%Forest	Varies with % of Forest land cover within a 600mt buffer around each site.	Continuous	71.61 (31.65, 96.20)	19.17
Road Density	Varies with road density (meters/sq.meters) within a 600mt buffer around each site.	Continuous	0.002 (0, 0.006)	0.001
Watershed-level:				
Distance from Major Dam (m)	Varies for each site with distance to a major dam (meters) along stream network	Continuous	54102.78 (25343.46, 76176.55)	18559.33

Distance from Small Dam (m)	Varies for each site with distance to a small dam (meters) along stream network	Continuous	6472.151 (1327.00, 12198.34)	2955.60
Dam Density	Varies with dam density (meters/sq.meters) in the HUC 10 watershed in which the site lies.	Continuous	0.00014 (0.00007, 0.00027)	0.00007
Habitat	Categorized as habitat falling under either of the two categories; National Forest land (1) and others (0)	Categorical-Binary	-	-
%Forest	Varies with % of Forest land cover within a HUC 10 watershed in which the site lies.	Continuous	64.20 (51.71, 82.01)	9.49
Road Density	Varies with road density (meters/sq.meters) within HUC 10 watershed in which the site lies.	Continuous	0.003 (0.002, 0.007)	0.002
DETECTION:				
(.)	Detection assumed to be constant			
Observer	Varies with observer that performed the survey (n = 3)	Categorical	-	-
Julian Day	Varies with Julian day measured during the survey	Continuous	189.6 (123, 260)	50.48
Air Temperature (°C)	Varies with mean air temperature measured during the survey	Continuous	27.07 (21.28, 35.00)	3.49
Water Temperature (°C)	Varies with mean water temperature measured during the survey	Continuous	22.65 (16.83, 28.00)	3.33
Average Depth (cm)	Varies with mean average depth measured during the survey	Continuous	16.26 (6.90, 40.30)	10.07

Table 3-3: Estimated detection (p), occupancy (Ψ) along with 95%CI and naïve occupancy for eight freshwater mussels species encountered at 15 sites in Savannah river basin South Carolina. Elliptio spp. complex refers to *E. complanata*, *E. icterina*, *E. angustata*, *E. producta*.

Species	**Estimated *p* ± SE**	**95% CI**	**Estimated *Ψ***	**95% CI**	**Naïve *Ψ***
Elliptio spp. complex	1.0 ± 0.00	1.0-1.0	0.53 ± 0.13	0.30 - 0.76	0.53
Alasmidonta varicosa	0.61 ± 0.18	0.26-0.88	0.14± 0.09	0.034 - 0.41	0.13
Lampsilis cariosa	0.27 ± 0.20	0.04-0.74	0.19± 0.15	0.03 – 0.62	0.13
Pyganodon cataracta	0.66 ± 0.14	0.35-0.87	0.21 ± 0.1	0.067 - 0.48	0.20
Strophitus undulatus	0.61± 0.13	0.35-0.82	0.27 ± 0.12	0.11 – 0.54	0.26
Uniomerus carolinianus	0.56 ± 0.15	0.27-0.82	0.21 ± 0.11	0.068 – 0.49	0.20
Villosa delumbis	0.75 ± 0.08	0.55-0.87	0.47 ± 0.13	0.24 – 0.71	0.46
Lasmigona decorata	0.66 ± 0.14	0.35-0.87	0.21 ± 0.1	0.067 – 0.48	0.20

Table 3-4: Top-ranked single-season models (ΔAIC_c or $\Delta QAIC_c < 4$) explaining site occupancy and detection of freshwater mussel species in the Savannah River Basin, South Carolina. (The estimates are accompanied with standard error followed by the lower 95% CI and the upper 95% CI). Models for certain species were corrected for overdispersion (global model with ĉ > 1) and were evaluated using $QAIC_c$ followed with inflation of standard errors and are indicated by using an asterisk *.

Top Candidate Models by species	**$\beta_i \pm$ SE (95% CI)**	**AICc/ QAICc**	**ΔAICc/ ΔQAICc**	**wi**	**K**	**Model Averaged $\Psi \pm$ SE (95%CI)**
Elliptio spp. complex						
Ψ (AvgW +%Swift), *p* (.)	14.65 ± 9.90 (-4.95 to 34.06) 6.97 ± 4.60 (-2.14 to 15.99)	17.33	0.00	0.436	4	0.53 ±0.38 (0.0 to 1.0)
Ψ (Sub H'), *p*(.)	3.64 ± 2.29 (-0.88 to 8.12)	18.74	1.41	0.215	3	
Ψ (Sub H' + AvgW), *p*(.)	2.67 ± 1.81 (-0.91 to 6.21) 2.63 ± 2.38 (-2.08 to 7.30)	19.35	2.02	0.159	4	
Ψ (Dam Den), *p*(.)	-2.27 ± 1.09 (-4.42 to -0.15)	20.22	2.89	0.103	3	
Ψ (Cond), *p*(.)	2.85 ± 1.64 (-0.40 to 6.06)	20.55	3.22	0.087	3	
Alasmidonta varicosa *						
Ψ(.), *p*(.)		15.97	0.00	0.816	2	0.14 ±0.15 (0.0 to 1.0)
Ψ (AvgW), *p* (AvgD)	2.25 ± 1.47 (-0.65 to 5.12)	19.91	3.94	0.114	4	

Lampsilis cariosa						
Ψ (.), *p*(.)		26.45	0.00	0.227	2	0.47± 0.16 (0.16 to0.78)
***Ψ* (Habitat), *p* (AvgD)**	72.82 ± 10.00 (53.02 to 92.42)	26.54	0.09	0.217	4	
Ψ (Dam Den), *p* (AvgD)	-5.57 ± 23.06 (-51.23 to 39.63)	26.64	0.19	0.206	4	
Ψ (%Forest600m), *p* (AvgD)	1.09 ± 2.51 (-3.89 to 6.02)	26.93	0.48	0.179	4	
Ψ (%ForestHUC), *p* (AvgD)	393.07 ± 10.00 (373.2 to 412.67)	27.01	0.56	0.172	4	
Pyganodon cataracta*						
Ψ (.), *p*(.)		26.06	-0.00	0.548	2	0.21± 0.13 (0.0 to 0.46)
***Ψ* (AvgW), *p* (Air Temp)**	2.14 ± 1.27 (-0.37 to 4.63)	28.05	1.99	0.203	4	
Ψ (Sub H'), *p* (Air Temp)	3.36 ± 2.73 (-2.06 to 8.72)	28.79	2.73	0.140	4	
Ψ (Dam Den), *p* (Air Temp)	-3.15 ± 4.12 (-11.31 to 4.92)	29.27	3.21	0.110	4	
Strophitus undulatus						
***Ψ* (Dam Den), *p*(.)**	-4.19 ± 3.80 (-11.71 to 3.25)	39.38	0.00	0.514	3	0.27± 0.20 (0.0 to 0.66)
Ψ (Small Dam), *p*(.)	2.15 ± 1.28 (-0.38 to 4.65)	40.67	1.29	0.267	3	
Ψ (Sub H'), *p*(.)	2.65 ± 1.91 (-1.13 to 6.40)	41.88	2.50	0.147	3	
Ψ (.), *p*(.)		43.40	4.02	0.069	3	
Uniomerus carolinianus*						
Ψ (.), *p*(.)		21.20	0.00	0.652	2	0.24± 0.15 (0.0 to 0.53)
***Ψ* (AvgW), *p* (AvgD)**	5.78 ± 6.42 (-6.94 to 18.37)	23.77	2.57	0.180	4	
Ψ (Major Dam), *p* (Avg.D)	-1747.40 ± 10.0 (-1767.20 to -1727.80)	24.93	3.73	0.101	4	
Villosa delumbis						

Ψ (Cond), *p* (AvgD)	6.27 ± 4.24 (-2.12 to 14.58)	46.32	0.00	0.456	4	0.50 ± 0.35 (0.0 to 1.0)
Ψ (Dam Den), *p* (AvgD)	-302.60 ± 26.89 (-355.84 to -249.90)	46.57	0.25	0.402	4	
Ψ (AvgW), *p* (AvgD)	2.25 ± 1.20 (-0.13 to 4.61)	49.53	3.21	0.092	4	
Lasmigona decorata*						
Ψ (.), *p*(.)		30.56	0.00	0.450	2	0.22 ± 0.21 (0.0 to 0.63)
Ψ (AvgW), *p* (Water Temp)	2.19 ± 1.38 (-0.54 to 4.89)	31.84	1.28	0.237	4	
Ψ (Sub H'), *p* (Water Temp)	3.38 ± 2.76 (-2.09 to 8.79)	32.75	2.19	0.151	4	
Ψ (Dam Den), *p* (Water Temp)	-3.13 ± 4.19 (-11.42 to 5.08)	33.40	2.84	0.109	4	
Ψ (Small Dam), *p* (Water Temp)	0.82 ± 0.75 (-0.67 to 2.30)	34.81	4.25	0.054	4	

Figure 3-1: Map of the Savannah river basin, South Carolina with locations of 15 freshwater mussel sampling sites. Savannah river basin is represented by the bold black outline and streams and creeks are represented by thin grey lines. The inset photo represents typical freshwater mussel micro-habitat.

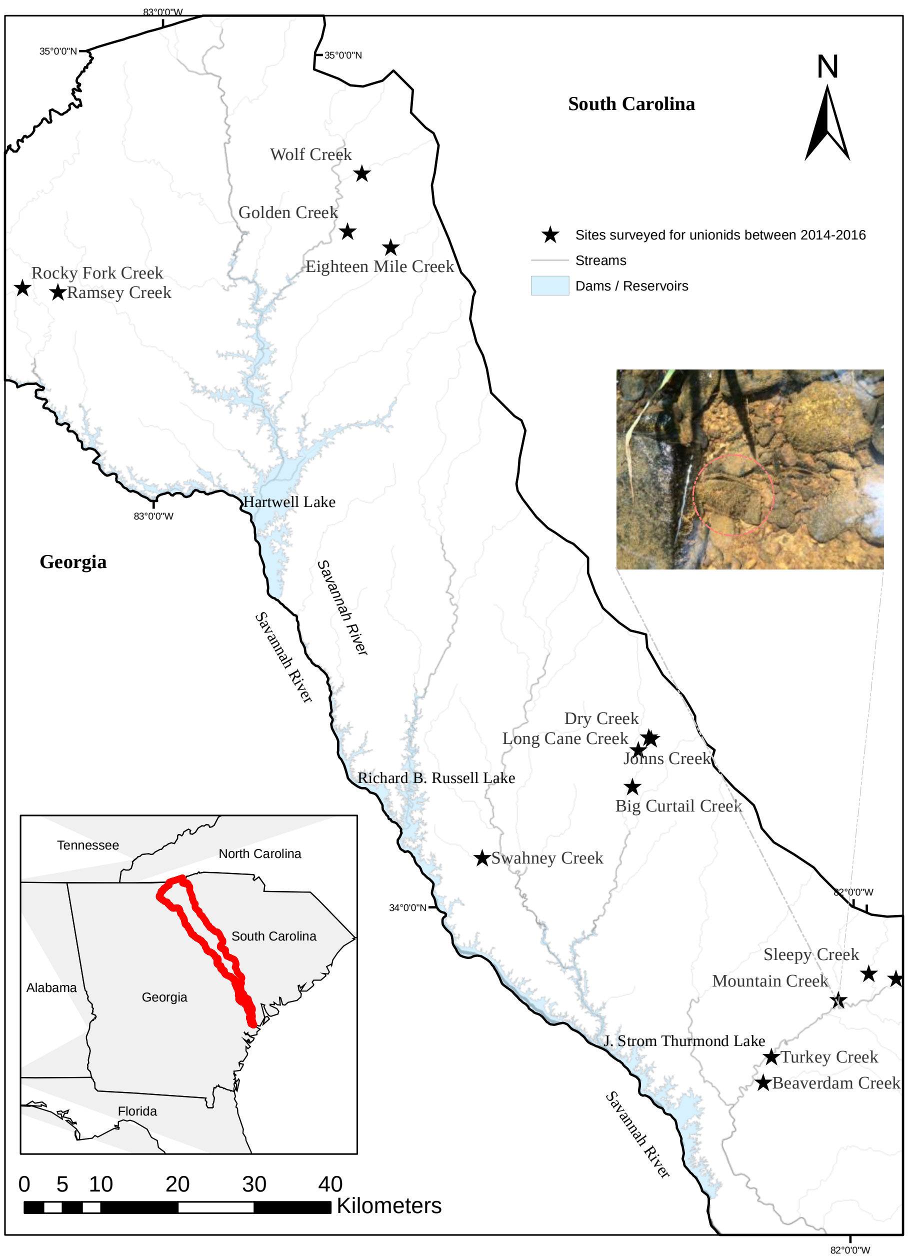


Figure 3-2: Naïve and estimated occupancy probabilities for freshwater mussel species encountered at 15 sites in Savannah River, South Carolina.

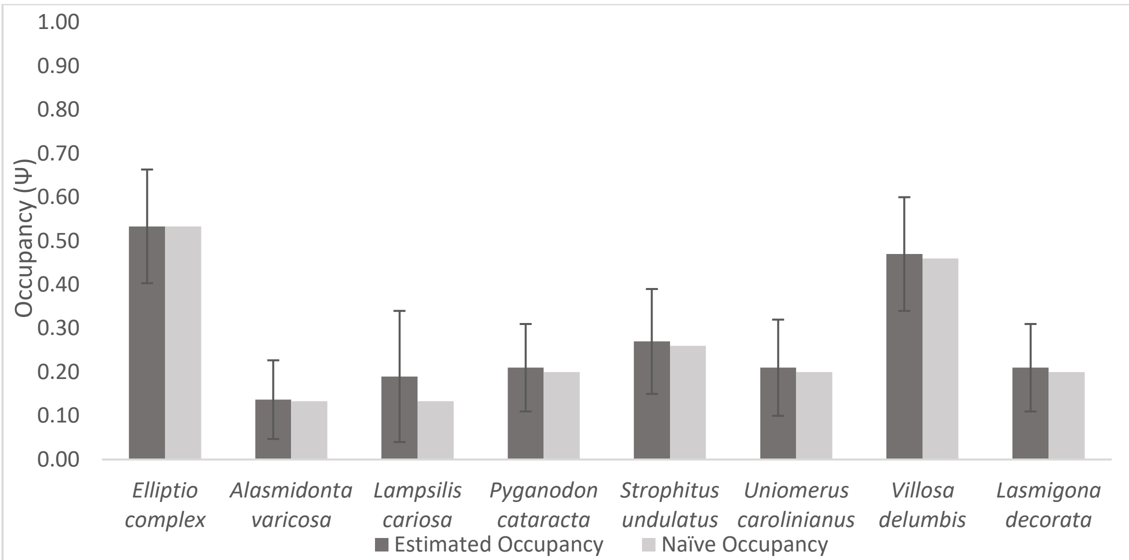
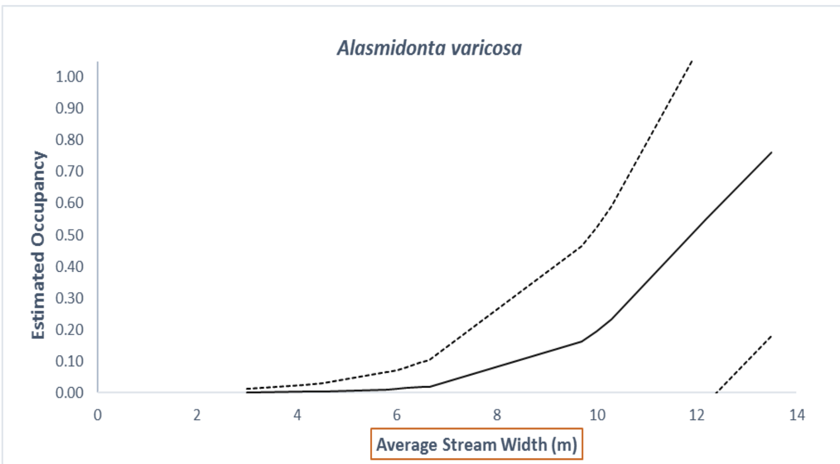
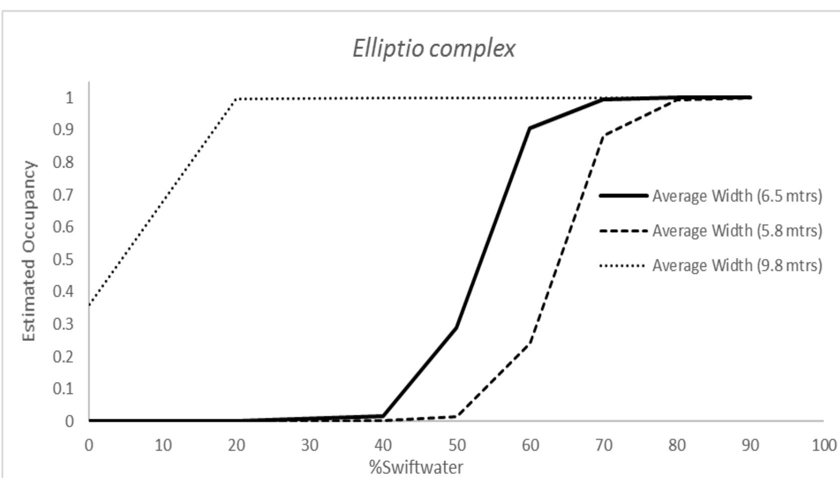


Figure 3-3. Estimated site occupancy of freshwater mussel species in Savannah River, South Carolina as a function of local and landscape-level covariates which featured in the best-approximating model of species specific candidate sets (ΔAIC_c or $\Delta QAIC_c < 2$) (dashed lines indicate 95%CI around these estimates).

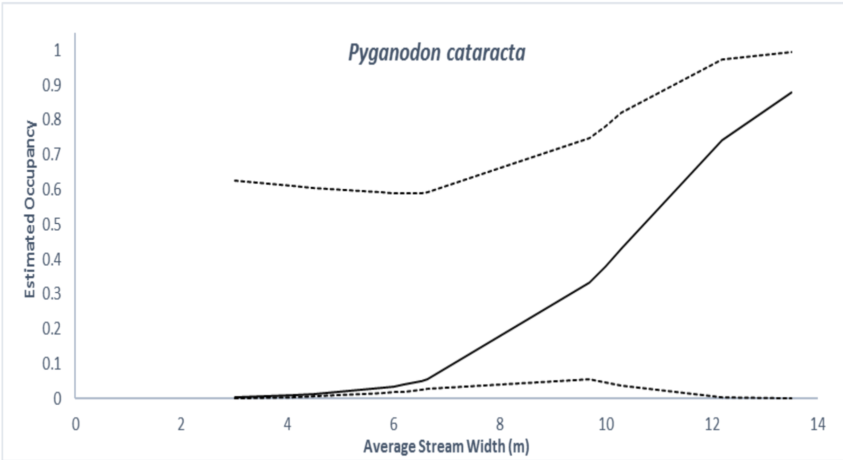
a)



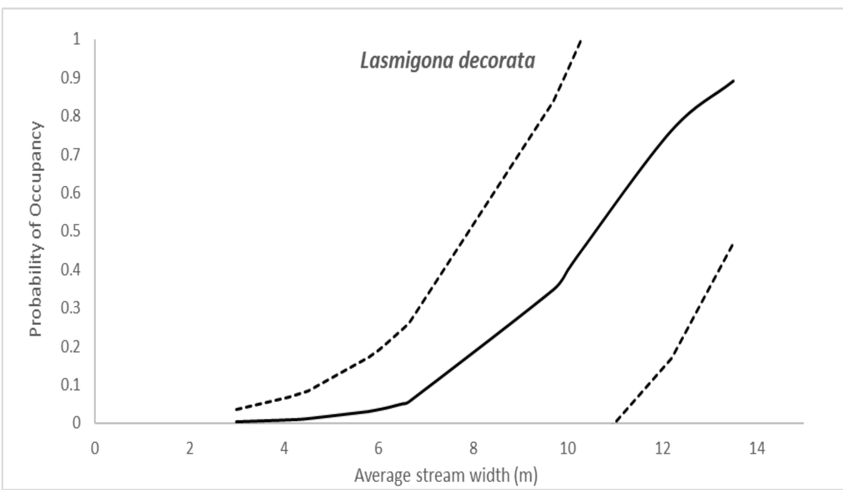
b)



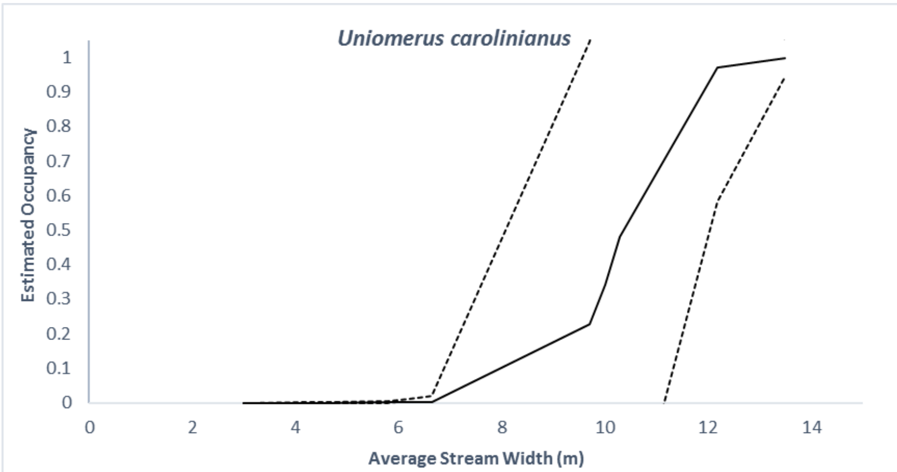
c)


Pyganodon cataracta
Estimated Occupancy
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
14
Average Stream Width (m)

d)

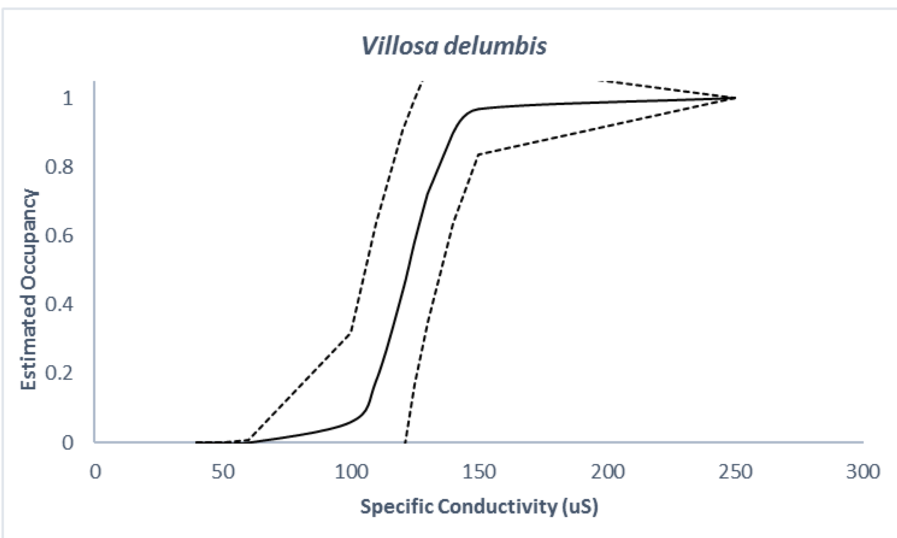

Lasmigona decorata
Probability of Occupancy
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
14
Average stream width (m)

e)



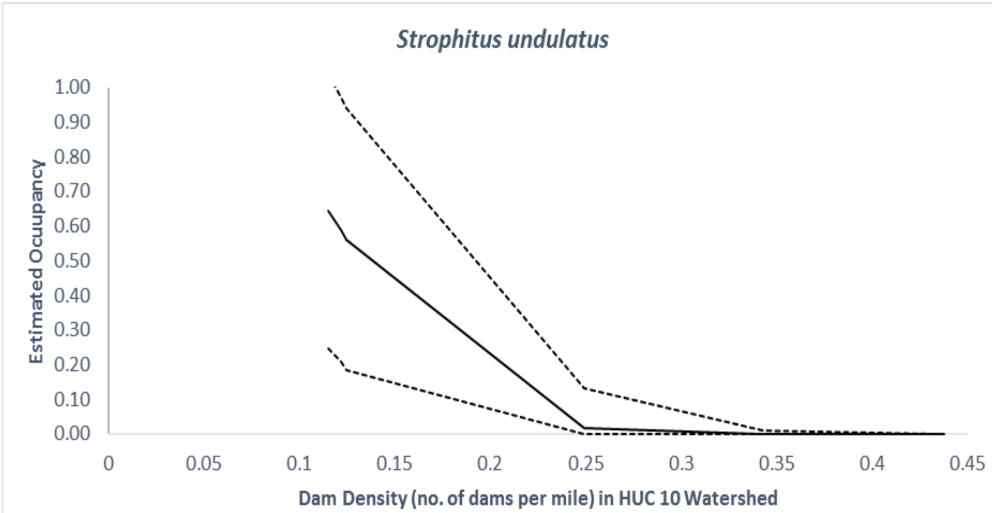
Uniomerus carolinianus
Estimated Occupancy
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
14
Average Stream Width (m)

f)

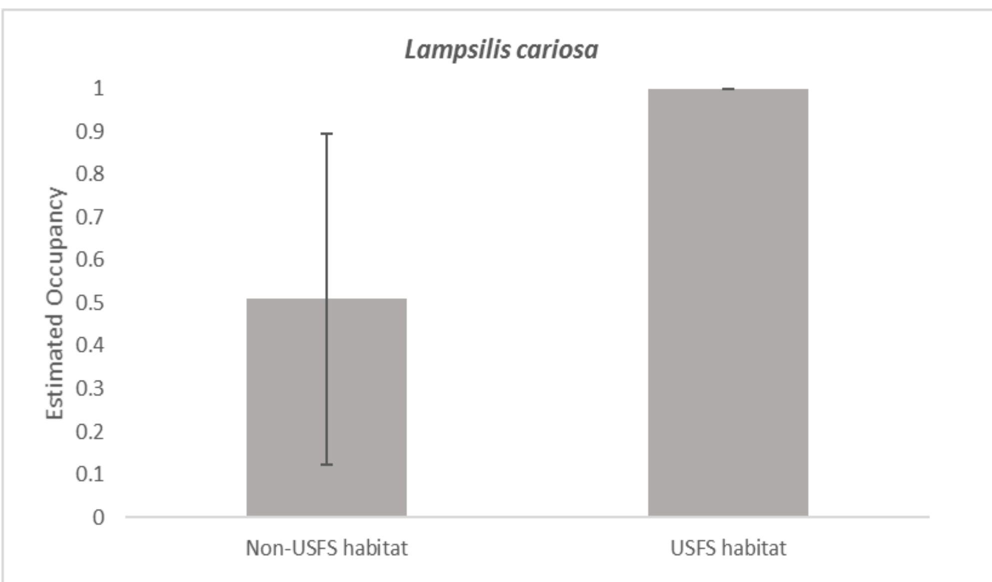


Villosa delumbis
Estimated Occupancy
1
0.8
0.6
0.4
0.2
0
0
50
100
150
200
250
300
Specific Conductivity (uS)

g)


Strophitus undulatus
Estimated Ocuupancy
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
Dam Density (no. of dams per mile) in HUC 10 Watershed

h)


Lampsilis cariosa
Estimated Occupancy
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Non-USFS habitat
USFS habitat

CHAPTER FOUR

APPLYING THE METAPOPULATION APPROACH TO QUANTIFY THE EFFECTS OF HABITAT DEGRADATION AND FRAGMENTATION ON FRESHWATER MUSSELS: CASE STUDY OF AN ENDANGERED MUSSEL, CAROLINA HEELSPLITTER IN SOUTH CAROLINA

ABSTRACT

The increase in demand for water resources and the associated impact on stream flows and thermal regimes is in conflict with the requirements of in-stream biota, particularly freshwater mussels. The Carolina heelsplitter (*Lasmigona decorata*) is a federally endangered species restricted to a few relict local populations in streams of North and South Carolina. Mussel populations have undergone significant declines in the recent times primarily attributed to anthropogenic activities such as urbanization, agriculture, land use change and waterway alterations (e.g. channelization's and impoundments). We constructed a spatial stage-structured stochastic model to determine the viability of the Carolina Heelsplitter metapopulation persistence under the threats of habitat loss triggered by habitat degradation, habitat fragmentation and a combined effect of both. The baseline simulation predicted that Carolina heelsplitter metapopulation has 0.00 probability of extinction during the next fifty years for the hypothetical metapopulation with initial abundance N_0=1008 and a moderate extinction risk with a probability of decline below threshold being 0.5778 for the best-estimate metapopulation with initial abundance N=60. Still, current threats such as habitat loss due to

impoundments, channelization and stream alterations make this species extremely susceptible to any change. Simulations of mussel decline under different scenarios of habitat loss indicated that the relative risk of extinction increased drastically with increased habitat degradation across both population systems, with the response being more severe for the best-estimate metapopulation N=60 (probability of decline below threshold =0.9634) as compared to the hypothetical metapopulation N_0=1008 (probability of decline below threshold = 0.398).

Keywords: RAMAS, metapopulation, impoundments, habitat degradation, fragmentation, freshwater mussels, extinction risk.

INTRODUCTION

Several anthropogenic factors are triggering habitat loss through habitat degradation and fragmentation causing decline in natural populations of species. Non-random species losses and changes in community structure are occurring at a rapid pace due to environmental changes coupled with anthropogenic stressors (Larsen et al., 2005; Schläpfer, Pfisterer, & Schmid, 2005). Species which are most susceptible to extinction are also those who have small, fragmented populations limited by dispersal. The southeastern United States is experiencing severe periods of drought along with escalating urban development resulting in large scale impoundment of rivers and streams to meet the increasing water demands for agriculture, industry and municipalities (Gangloff, Siefferman, Seesock, & Webber, 2009; Peterson, Wisniewski, Shea, & Jackson, 2011b; Vaughn & Taylor, 1999). Increased anthropogenic water demands will threaten the water security for many aquatic species across the southeastern United States.

Freshwater mussels are long-lived, sessile, filter-feeding invertebrates belonging to family Unionidae and are widely distributed in North America with 297 recognized taxa (Williams et al., 1993). Of these 297 known taxa, only 70 are stable (William et al 1993). Freshwater mussels are among the most threatened groups of organisms in North America and are continuously experiencing sharp decline in diversity and richness. Southeastern US has the highest species diversity of freshwater mussels than any other region of the world (Lee & DeAngelis, 1997; Lydeard & Mayden, 1995; Williams et al., 1993). They require steady stream flows with ambient water quality and quantity, stable substrate to provide refugia and host fish for consistent recruitment and dispersal (Galbraith & Vaughn, 2011; Layzer & Madison, 1995; Schwalb et al., 2011; Strayer & Ralley, 1993) and the loss of which can drive freshwater populations to extirpation. In the last 75 years, the prime factors causing the stream habitat loss are the large-scale impoundment and channelization of rivers and streams (Bogan, 1993). Dams and impoundments vary in effect on aquatic systems; low head dams with small impoundments offer some passability or permeability to aquatic species such as migrating fish whereas high dams with large impoundments act as complete barriers (Fuller, Doyle, & Strayer, 2015). These effects of impoundments and channelization result from two main factors; habitat fragmentation, or loss of structural and functional connectivity which can be physical/physiochemical/biological barriers to longitudinal movement of organisms; and habitat degradation caused by inundation of upstream habitat, altered amounts and timing of flows downstream, disruption of the thermal regimen and substrate modification all of which has serious repercussions on freshwater mussel metapopulations by reducing its survival, recruitment and dispersal ((Fuller et al., 2015)Lytle & Poff, 2004; Peterson et al., 2011b; Strayer et al., 2004; Vaughn & Taylor, 1999). The effects of road runoff on aquatic ecosystems is not well studied though its effects are similar to that of urban runoff but with higher concentration of pollutant and debris being introduced to these systems (Pitt & Field, 1990). The stormwater runoff, maintenance activities of roads and highways as well as maintenance and upkeep of bridges introduces several pollutants, sediments and debris leading to pollution barriers whereas culverts and road crossings act as physical barriers by being highly impermeable to passage of organisms, both of which degrade and fragment suitable mussel habitat within the streams and rivers (Alderman, 1998; Fuller et al., 2015).

Freshwater mussels can occur either as dense aggregations called mussel beds or as discrete patches within otherwise unsuitable habitat mosaic; both occurrences represent sub-populations or local populations. These local populations are connected by colonization-extinction events aided by dispersing host fish, forming a metapopulation within a riverine ecosystem (Strayer et al., 2004). Freshwater mussels also exhibit extinction-debt in response to stressors such as habitat loss where the current extinctions are happening because of a delayed result of habitat degradation or fragmentation or both (Newton et al., 2008). Unlike fish and other macroinvertebrates, mussels exhibit limited movement and occupy the same sediment bed for most of their adult lives having limited refugia from habitat degradation (Vaughn and Taylor, 1999). The fragmentation of the mussel habitat into discrete patches can lead to dispersal barriers which the host fish may not be able to overcome to colonize the local patches thereby triggering the metapopulation decline. Habitat degradation and fragmentation are important factors determining the population dynamics and spatial distribution of freshwater mussels and hence this research paper focuses on assessing the impacts of habitat degradation and fragmentation on population viability of freshwater mussels.

Population viability analysis (PVA) is a popular tool used in conservation biology for assessing the status and management of threatened and endangered species. It evaluates and synthesizes data and demographic and spatial information about a species and involves developing models that best characterize the species life history and gives in probabilistic terms the likelihood that a population will persist for a randomly chosen number of years (Beissinger & McCullough, 2002; Beissinger & Westphal, 1998; Boyce, 1992; Keedwell, 2004). It also allows for simulations of the population persistence under different management and catastrophic scenarios which help in assessing the effects of habitat quality, habitat patches, fragmented populations and rates of dispersal between habitat patches and effects of inbreeding depression (Keedwell, 2004). We utilized a similar approach to synthesize the available information to develop a metapopulation model for assessing the population viability of native endangered freshwater mussel, Carolina Heelsplitter under the scenarios of habitat degradation, habitat fragmentation and a combined effect of both. A better understanding of these stressors on the persistence of the Carolina Heelsplitter metapopulation can help identify and prioritize conservation, management and reintroduction strategies for the species and its critical habitat.

Study Species

The Carolina heelsplitter (*Lasmigona decorata* [Lea, 1852]; Figure 4) is a large ovate Atlantic Slope freshwater mussel species belonging to the family Unionidae. It occurs in shallow forested streams and rivers with a heterogenous, stable stream banks and excellent water quality (Alderman, 1998) The Carolina heelsplitter feeds by siphoning and filtering food particles from the water column as is characteristic with other freshwater mussels. The complex life cycle of the species is like other species in the family Unionidae. The sperm released by males is taken up by the female during the siphoning action and the fertilized eggs are brooded by females till the larval form completes development. The female mussels utilize elaborate mantle lures to attract host fish to deliver the larval glochidia which act as obligate parasites on the host fish. The glochidia metamorphose into tiny mussels which detach from the host fish and continue the rest of the life cycle as sedentary mussels attached to the substrate at the bottom of the stream (Haag, 2012b; USFWS, 2011). Several species of minnows (Cyprinidae) and sunfish (Centrarchidae) have been identified as potential hosts for Carolina Heelsplitter through laboratory trials (Eads, Bringolf, Greiner, Bogan, & Levine, 2010).

Historically the Carolina heelsplitter occurred in several locations in the Catawba, Pee Dee, Saluda, and Savannah River systems in North and South Carolina. Anthropogenic activities such as dam construction, silviculture, agriculture, urbanization, mining, road construction and maintenance and discharge of pollutants have been attributed to the decline of the Carolina heelsplitter throughout its range in North and South Carolina (Alderman, 1998; USFWS, 2011). Currently it has a fragmented distribution with 10 extant populations being restricted to the Goose Creek/ Duck Creek and Flat Creek/Lyches River in the Pee Dee river system, the Waxhaw Creek, Sixmile Creek, Gills Creek/Cane Creek, Fishing Creek/South Fork Fishing Creek and Bull Run Creek (Rocky Creek) in Catawba River system, Red Bank Creek in Saluda river system and Turkey Creek and Cuffytown Creek in Savannah River system (Alderman, 1998; USFWS, 2012). Habitat loss in the form of habitat degradation and habitat fragmentation appears to be the causal factor in the decline and range contraction of the Carolina Heelsplitter, thus leading to the species being categorized as federally endangered since June 30, 1993.

METHODS

Study Area

The scope of the analysis was limited to the Turkey Creek population (Figure 4-2) in Edgefield and McCormick Counties, South Carolina which includes the local populations inhabiting the isolated stretches of Turkey Creek, Sleepy Creek, Mountain Creek, Beaverdam Creek and Little Stevens Creek. The Turkey Creek watershed contains a large portion of the Sumter National Forest and falls within the Savannah-piedmont ecobasin. This watershed harbors several endemic freshwater mussel and fish species and is one of the most biologically significant tributary in the entire Savannah River Basin

(Alderman, 1998) and used to contain extensive areas of optimal habitat that once supported large populations of Carolina Heelsplitter. However now it serves as refugia to small local populations which are restricted to short stream reaches and are extremely susceptible to stochastic events (USFWS, 2012). These above-mentioned river systems form the critical habitat for Carolina Heelsplitter encompassing a total of 148.4 stream kilometers in North and South Carolina (USFWS, 2002).

Carolina Heelsplitter Metapopulation Model for Demographic Simulations

We developed a minimalistic spatially-structured stage-classified matrix metapopulation model for the Carolina Heelsplitter metapopulation in the Turkey Creek watershed in Savannah River Basin, SC (Table 4-1). In developing the model and determining the parameter values we used data from the occupancy surveys conducted between 2014 to 2016 (Mhatre et. al., 2017 unpublished manuscript), previously published data on Carolina heelsplitter (Alderman, 1998; USFWS, 2012) and via personal communication with freshwater mussel expert Morgan Wolf, USFWS South Carolina field office. We used the program ARC GIS and the tools Spatial Analyst and Network Analyst (ESRI, 2016) to identify suitable habitat patches, location of the patches and distance between patches and linked this landscape data to the metapopulation model (Figure 4-2).

Stage Matrix

Very little information about Carolina Heelsplitter reproductive biology and life history of the various life stages is known. This model assumes that the life history of the mussel can be characterized as a series of transitions between discrete stages. In this stage-structured model (Lefkovitch matrix), individuals in a mussel metapopulations are grouped into classes based on their developmental state (Akcakaya et al., 2004). The life cycle of a freshwater mussel is divided into the following stages: 1) recruits (Age 0 or glochidia/larval stage) 2) pre-reproductive juveniles (Age 1-2) and 3) reproductive stage consisting of adults (Age 3 to 15). Mussels belonging to Genus *Lasmigona* (Tribe Anodontini) exhibit periodic type of life history with early sexual maturity at ages 2 or 3 and are short-lived with average life expectancy being 15 years (Haag, 2012; Haag and Staton,2003; Morgan Wolf, USFWS, Personal comms). A population projection matrix contains an array of probabilities associated with each transition, as well as fecundity values representing the reproductive output of each mature stage. We parametrized the model assuming post-breeding census with all the stages being included in the census and sex structure was females only. Since information on survival for the three stages is difficult to summarize, we used information available for surrogate species belonging Tribe Anodontini to make inferences about the survival and fecundity to fill the stage matrix. The survival of recruits transiting into juveniles, $S_j = 0.74$, the survival of juveniles was divided into juveniles staying as juveniles for 1 year, $S_{j\text{-}j} = 0.37$ and Juveniles transitioning into adults, $S_{j\text{-}a} = 0.37$ and survival of adults, $S_a = 0.5555$(Haag & Leann Staton, 2003; Haag, 2012). Fecundity in freshwater mussels is usually defined as the number of glochidia per gravid female mussel (Haag, 2002). Haag (2013) provides an estimate for the annual fecundity of North American mussel species which vary widely ranging from < 2000 to 10 million. However, in the metapopulation stage matrix, we wanted to define fecundity as the net reproductive success of the female mussel, which involves the processes of spawning, release of glochidia, attachment of glochidia to suitable host fish, metamorphosis of glochidia into juveniles and release of viable mussel to continue the life cycle (Jones et.al 2012). In absence of human induced impacts, mussel display population growth rate of $\lambda = 1$ (Haag, 2012; Villella, Smith, & Lemarie, 2004), hence the fecundity (F_{a}) was determined iteratively in the stage matrix until the desired stable $\lambda=1$ was obtained. The stage matrix for the Heelsplitter model was the same for both populations (Figure 4-3).

Carrying Capacities and Initial Abundances

For both populations, each local population has a unique initial abundance and the initial distribution of each population was set to its stable distribution based on stage matrix for that population. We used carrying capacities to model ceiling-type of density dependence for both simulations. The density dependence affects all vital rates for all the four stages and is population–specific type and is based on the total abundance of all stages. The model allows populations to fluctuate independent of population density with respect to the stage and standard deviation matrices until the population reaches ceiling. At this point the population remains at this level until a population decline takes it below the ceiling value. The carrying capacities (K) were set to hypothetical value of 1000 for each patch in both simulation sets. Patches with higher habitat quality had a higher carrying capacity (K) as compared to patches with lower habitat quality. Habitat quality declined with increasing degradation and fragmentation and this resulted in lower carrying capacities. The quality of the habitat was determined by superimposing the patch location with land use, road density and presence of small dams in ARC GIS.

Stochasticity

Stochastic factors can impact population dynamics in several ways, the most important of which are demographic stochasticity and environmental stochasticity. We modeled demographic stochasticity by drawing number of survivors to reach each stage from a binomial distribution, while reproductive output was modeled with a Poisson distribution (Akçakaya, 1991; Brillinger, 1986). There is not sufficient information on the variation in the life stages. Hence based on our understanding of mussel biology and ecology we supposed the coefficient of deviation (CV) for survival to be 5% and fecundity to be 10%. We used the autofill option in RAMAS METAPOP to obtain the standard deviation matrix based on the abovementioned values. The environmental stochasticity accounts for the fact that the demographic parameters in the projection matrix vary with time. We modeled environmental stochasticity by assuming that the parameters vary according to random log-normal distribution with specified means and standard deviations.

Correlation-Distance Function

If the factors that determine environmental stochasticity are often spatially autocorrelated, it may be more reasonable to impose correlations in the stochastic realizations of projection matrices in nearby patches. This is done by defining a correlation function that decays exponentially with distance downstream (Akcakaya et al., 2004; Gilpin, 1990). Streams are usually positively spatially autocorrelated among sites, at least at small spatial scales (100 m) (Newton et al., 2008; Wilkinson & Edds, 2001). The Turkey Creek watershed is a relatively small study area; hence it is fair to assume that any disturbance activity such as habitat degradation and fragmentation will be strongly spatially autocorrelated and that the metapopulation dynamics are affected by this correlation. In our model, we did not utilize the negative exponential function and instead manually input correlation probabilities in the correlation matrix. We used two estimates of correlation, high correlation and low correlation to set the correlation of vital rates among population. We assumed that the correlation of patches within the same stream system was 50% and that of patches amongst the stream systems was 25%.

Dispersal-Distance Function

This model assumes that Carolina heelsplitter local populations inhabiting the habitat patches are a part of a Turkey creek heelsplitter metapopulation. The mussel local populations have potentially limited connectivity due to host fish dispersal and presence of barriers. Dams will constitute dispersal barriers, reducing dispersal between patches separated by dams to near zero. In case of freshwater mussels, adults are incapable of dispersal and the dispersal parameters are applied to the recruit stage only. In our model dispersal is defined as the movement of recruits via host fish from one population to another and is modeled such that as distance between local populations increase the dispersal rate for recruits decreases. Dispersal rates specified as the proportion of dispersing individuals per time step from one population to another depends on the distance between the populations (Akçakaya, 2005). RAMAS METAPOP gives the dispersal distance function as $M_{ij} = a * exp(D_{ij}\ c/b)$, where M_{ij} is the dispersal rate of between population i and j, D_{ij} is the distance between the source and target patches and b is a constant representing the average distance a disperser travels and a and c are constants. Our model was fitted to this dispersal distance function, by specifying a= 1 (Reference scenario), b = 300 m and D_{max} = 3000 m (Figure 4-4). The parameter b determines the rate of decline in the number of dispersers as distance increases. Our value of b= 300 was chosen based on average dispersal distance for fish belonging to families Cyprinidae and Centrarchidae (Eads et al., 2010; Schwalb et al., 2011). Similar to previous studies on impacts of habitat loss and fragmentation (Akçakaya & Raphael, 1998; Shriver & Gibbs, 2004), in absence of information to vary a according to the total proportion of dispersers between populations, we used different values of a for simulating the four scenarios, for reference scenario a=1, for habitat degradation scenario a=1, for habitat fragmentation scenario a =0.5 and for the combined effect scenario a=0.3. We incorporated demographic stochasticity in dispersal among populations by sampling several dispersers from a binomial distribution with a sample size equal to the number of recruits in the source population and probability equal to dispersal rate based on distance. We chose the coefficient of deviation (CV) for dispersal to be 25%.

Habitat Loss: Quantifying effects of Degradation and Fragmentation

We modeled habitat loss by dividing its effects into habitat degradation, habitat fragmentation and combined effect of habitat degradation and habitat fragmentation. This resulted in a gradual decline in the carrying capacities, survival and fecundity rates and dispersal rates of all populations. The change in the vital rates and dispersal rates for a given scenario were estimated from literature review and threat analysis of the existing Carolina heelsplitter populations (Alderman, 1998; Peterson et al., 2011b; Schwalb et al., 2011; USFWS, 2012). The relative decline was not the same for all populations. Because the changes in vital and dispersal rates in response to habitat loss are at best educated guesses, the aim of this analysis is not the exact time to metapopulation extinction but rather to show the severity of the impacts of anthropogenic disturbances to habitat on the Carolina heelsplitter metapopulation persistence.

Sensitivity Analysis

Sensitivity analysis is useful for determining which parameters need to be estimated more carefully. To account of uncertainty around the demographic and dispersal parameters we performed sensitivity analysis on five model parameters, stage matrix means, stage matrix standard deviations, initial abundance, carrying capacities (K) and dispersal rate using the Sensitivity Analysis program of RAMAS GIS. We varied the vital rate parameters by $\pm$ 10% and the dispersal rate by $\pm$ 50% to assess the degree to which the deviations in each affected metapopulation persistence for all four scenarios. The results of sensitivity analysis are presented as risk of metapopulation falling below the extinction threshold of 100 individuals in absolute term and as a percentage of the results with the initial (baseline) value of the parameter.

Model Development and Scenarios

We utilized the software package RAMAS METAPOP (Akçakaya & Root, 2005) to analyze the effects of habitat loss on viability of the Carolina heelsplitter metapopulation in the Turkey creek watershed in Savannah Basin, SC. The model results were summarized by implementing indices such as mean abundance through time, metapopulation occupancy (number of occupied patches) through time and risk/probability of 90% percent decline as a function of amount of decline and time to quasi-extinction (time to fall below the metapopulation extinction threshold). All the results are provided with their 95% confidence interval.

For our analysis, the Carolina heelsplitter model features two metapopulations with different initial abundances; one with N_0 =1008 and other with N = 60. The first metapopulation is a hypothetical example that assumes a healthy initial population of Carolina heelsplitter in the Turkey Creek watershed, N_0 =1008, (NatureServe, 2011). Surveys conducted by USFWS from 2008-2011 within the Turkey Creek Watershed, SC estimated the population size to be N=30 (USFWS, 2012). However, the entire watershed was not sampled and only partial surveys were conducted of the occupied streams by the USFWS, hence the total number of individuals recorded would be expected to be slightly higher if more extensive surveys of these streams were conducted. Hence for this analysis, the second metapopulation assumes an initial population size of N=60 as an effective population size within the designated critical habitats of the Turkey Creek watershed.

Each metapopulation features four scenarios which were evaluated by running 5000 iterations on an annual time step for 50 years;

1) Reference (REF) or baseline scenario which implies all patches have same carrying capacities and $\lambda = 1$.
2) Habitat Fragmentation (HF) scenario which implies loss of connectivity between patches hence the relative dispersal between patches is low.
3) Habitat Degradation (HD) scenario which implies that some patches have degraded habitat which has resulted in reduced carrying capacities, low relative fecundity and low relative survival for all life stages.
4) Combined effect of Habitat Degradation and Fragmentation characterizing total Habitat Loss which implies patches have low carrying capacities, low dispersal, low relative survival and low relative fecundity for all life stages.

In the reference scenario, no change was made to any demographic parameter. All populations had same initial abundances with relative dispersal, fecundity and survival =1.0. Under dispersal tab, a =1.0, b=300m (average distance travelled by host fish in meters), c= 1.0 and D_{max} = 3000 m. The correlation matrix, all local populations in same stream had 50% correlation, local populations in between streams had 25% correlation. To simulate the effect of habitat degradation (HD) changes were made to relative fecundity and survival for populations that seemed to be in areas of high road density or in proximity of a small dam. The relative survival varied from 1.0 (least affected) to 0.5 (most-affected). The fecundity varied similarly between 1.0 (least affected) to 0.3 (most affected). To simulate the effect of habitat fragmentation due to presence of barriers such as dams/ culverts or presence of road crossings (HF) changes were made to relative dispersal for some populations in path of the barriers as well as reduced *a*= 0.5 under the dispersal tab for this simulation. To simulate the combined or additive effect of both habitat degradation and fragmentation, effects of the two above scenarios on relative survival, fecundity and dispersal were combined along with reduced carrying capacities and the dispersal constant *a* was reduced to *a*=0.3. In this scenario, the most affected populations had relative survival was 0.5 and relative fecundity was 0.5 with relative dispersal 0.5. The moderately affected populations had relative survival was 0.5, relative fecundity was 0.8 and relative dispersal was 0.8 and least affected populations had relative survival, fecundity and dispersal = 1.0 (Refer Table 4-1).

To evaluate the impacts of habitat loss in form of habitat fragmentation, habitat degradation and a combined effect of habitat degradation and fragmentation, we first present results of the reference or baseline model which represents the current status of the Carolina Heelsplitter metapopulation within the Turkey creek watershed. We then compared the three habitat loss scenarios with the baseline model results to evaluate the impacts of habitat loss on Carolina heelsplitter metapopulation viability. We performed this step for both populations the hypothetical N_0=1008 and the real-time population N=60.

RESULTS

Sensitivity Analysis

The results showed extreme sensitivity to deviations in stage matrix means and subsequently population growth rate λ. A 10 % decrease in the stage matrix values increased the probability of quasi-extinction by 9,900% for the Reference and Habitat Fragmentation scenarios and by 250% and 230% for the Habitat Degradation and Combined effect scenarios respectively. It can be concluded that all four model scenarios are extremely sensitive to vital rates such as survival and fecundity. Increasing the initial abundance by 10% had a positive effect on metapopulation persistence and reduced the probability of quasi-extinction in the combined scenario by 94%. Increasing the dispersal rates by 10% increased the probability of quasi extinction for habitat degradation scenario by 105% and combined scenario by 103%. The four scenarios displayed little to sensitivity to the rest of the parameters tested (Table 4-2).

Patch Structure Analysis using ARC GIS

Using ARC GIS, for population system N_0=1008, the population size was equally divided in 72 local populations inhabiting the patches by utilizing the network analyst toolbox (Figure 4-2). After this distribution, each local population has an initial abundance of 14 individuals and set the initial distribution of each population to its stable distribution based on stage matrix for that population. For population N=60, the population size was equally divided within 15 local populations inhabiting the patches identified by ARC GIS and during the occupancy survey field work (unpublished Mhatre et al 2017).

The Hypothetical Metapopulation N=1008

In the baseline model, the mean abundance of the Carolina heelsplitter metapopulation decreased by 45.43% and has an expected minimum abundance of 509 (Figure 4-5 a). The number of occupied patches decreased from 72 to 30 by 58.33%. The model indicated no risk to the population falling below the extinction threshold of 100 individuals. Per the sensitivity analysis, the baseline model was highly sensitive to changes in survival and fecundity rates and was not affected by variation in any other tested parameters (Table 4-2). The simulated effects of habitat fragmentation (Scenario 2) resulted in 48% decline from the initial abundance with an expected minimum abundance of 482 individuals and a decrease in the metapopulation occupancy by 64% (Figure 4-5 a and Figure 4-6 a). The risk of 90% decline of Carolina Heelsplitter metapopulation due to habitat fragmentation was negligible (Figure 4-7 a and Figure 8). In the habitat degradation (scenario 3) model, the mean abundance decreased by 86% over 50 years with expected minimum abundance of 106 individuals and decrease in metapopulation occupancy by 91.5% (Figure 4-5 a and Figure 4-6 a). The probability of 90% decline was 0.398 with the time to quasi-extinction approximately being 49.3 years (Figure 4-7 a and Figure 8). In the presence of the final scenario 4 which simulated the combined effects of habitat degradation and habitat fragmentation, the probability 90% decline was very high (0.4340) and the time to quasi-extinction was approximately 49.1 years (Figure 4-7 a and

Figure 8). The mean abundance in this scenario decreased by 88% with an expected minimum abundance of 103 and a decrease in metapopulation occupancy by 91.5%(Figure 4-5 a and Figure 4-6 a).

Overall, the model results suggest that the Carolina heelsplitter metapopulation with N_0=1008, has a significantly higher risk of decline under the assumptions of habitat degradation and a combined effect of habitat fragmentation.

The Best-Estimate Metapopulation; N=60

In the baseline model, the mean abundance of the Carolina heelsplitter metapopulation with a real-time population size of N=60 decreased by 80% over 50 years and has an expected minimum abundance of 7 individuals (Figure 4-5 b). The number of occupied patches decreased by 93% (Figure 4-6 b). The model indicated a low risk (0.5778) to the population falling below the extinction threshold of 5 individuals and the time to quasi-extinction was more than 50 years. The simulated effects of habitat fragmentation (Scenario 2) resulted in 85% decline from the initial abundance and a 100 % decrease in the metapopulation occupancy (Figure 4-5 b and Figure 4-6 b). There is a moderate probability of 90% decline of Carolina Heelsplitter metapopulation due to habitat fragmentation was 0.6596 and the time to quasi-extinction was approximately 33.2 years. (Figure 4-7 b and Figure 8). In the habitat degradation (scenario 3) model, the mean abundance and metapopulation occupancy decreased by 100% over 50 years (Figure 4-5 b and Figure 4-6 b). The probability of 90% decline was 0.9634 with the time to quasi-extinction approximately being approximately 9.2 years (Figure 4-7 b and Figure

8). In the presence of the final scenario 4 which simulated the combined effects of habitat degradation and habitat fragmentation, the probability of 90% decline was very high 0.9976 and the time to quasi-extinction was approximately 8.7 years (Figure 4-7 b and Figure 8). The mean abundance and the metapopulation occupancy decreased by 100% indicating total metapopulation extinction by the end of 50 years (Figure 4-5 b and Figure 4-6 b).

Overall, the reference/baseline model results suggest that the Carolina heelsplitter metapopulation with N=60 is on a downward trajectory with a low to moderate risk of decline. The habitat fragmentation scenario indicates a moderate risk of metapopulation decline whereas under the assumptions of the habitat degradation and the combined effect of both the Carolina heelsplitter metapopulation has a significantly high risk of decline and probable extinction of the metapopulation.

DISCUSSION

The results from this metapopulation viability analysis do not represent the fate of the Turkey Creek Carolina heelsplitter metapopulation in the next 50 years. This analysis depicts the likely outcomes in form of probability of 90% decline of the habitat loss scenarios that we postulated. Our analysis revealed that for both population systems habitat loss primarily from habitat degradation has a pronounced negative effect of the Carolina heelsplitter metapopulation persistence than Habitat fragmentation which played a significant role in metapopulation decline only when the initial abundance or population size was low (Figure 7 and Figure 8). Our results indicate that survival and fecundity rates of Carolina heelsplitter could be highly sensitive to the secondary effects of habitat degradation and fragmentation and could vary with the life stages (recruits, juveniles and adults) of this species. It is a well-known fact that small populations are more susceptible to demographic and environmental stochasticities and allele effects increasing the probability of extinction and making the population more vulnerable (Beissinger & McCullough, 2002; Boyce, 1992; Hanski, 1998). A similar trend was observed in our analysis with the more conservative best-estimate metapopulation of Turkey Creek System N=60 being more vulnerable to the effects of habitat loss.

In our analysis, we accommodated uncertainty and variability in determining viability of endangered species. We incorporated 5%, 10% and 25% standard deviations in survival, fecundity and dispersal rates respectively. We incorporated environmental stochasticity and demographic stochasticity in reproduction, survival and dispersal to express the extinction probability of model scenarios. Even after accounting for uncertainties, our model parameters particularly demographic parameters were imprecise due to lack of data and previous literature of the elusive Carolina heelsplitter. In order to assess uncertainty in our model output, we used a medium estimate (from a range of high and low values) to estimate risks and used sensitivity analysis to estimate uncertainty of the parameters towards these risk estimates. The sensitivity of results to stage matrix means was not startling and all the scenarios showed heightened sensitivity to the vital rates, which means there is risk that the Carolina heelsplitter metapopulation persistence may be jeopardized if there are significant decline in the survival and fecundity rates (Table 4-2). A surprising relationship was the weak negative effect of variation in dispersal rate on metapopulation persistence. A similar effect was observed in studies by Akçakaya & Baur (1996), Akçakaya & Atwood (1997) and Stevens & Baguette (2008), were low dispersal improved the metapopulation persistence rate. In these studies, the source-sink dynamics came into play, with increase in dispersal distance the number of disperser increased from larger populations which acted as source to smaller sink populations which were more prone to extinction as a result of demographic stochasticity (Akçakaya & Baur, 1996; Akçakaya & Atwood, 1997; Stevens & Baguette, 2008). A similar type of effect seems to appear in our models with some smaller habitat patches with lower carrying capacities acting as sink populations. The metapopulation was not sensitive to other demographic parameters such as the standard deviations of stage matrices, carrying capacities and initial abundance. Our results highlight the need to obtain better estimates of vital rates and dispersal rates. Exhaustive surveys of all Carolina heelsplitter local populations could help obtain a range of vital and population growth rates that could better parametrize this model and move beyond the assumption that all local populations have the same population growth rate of λ=1.006.

Our model contained several assumptions and was intentionally simple with naïve approximation of the effects of habitat loss in terms of habitat degradation, fragmentation and a combined effect of the two. We did not account for any catastrophes as our study area is designated as a critical habitat for Carolina heelsplitter and has protection from human catastrophes such as sewage, mining and effluent runoffs. Environmental catastrophes such as droughts can have severe implications of the metapopulation persistence but was not within the scope of our analysis. Another shortcoming of our model was that it was unrealistic in the spatial distribution of populated sites. Mussels are elusive organisms and are usually burrowed deep within the substrate. The field survey conducted for occupancy studies in from 2014-2016 (Mhatre et. al. 2017, unpublished manuscript) helped us identify a few occupied habitat patches within the watershed, but it was far from exhaustive. The location of a most of the habitat patches has been summarized by using ARCGIS Spatial and Network Analyst toolbox.

We modeled habitat degradation by reducing the carrying capacities and relative survival and fecundity of the degraded patches. Several studies have documented declining survival and reproduction rates of mussels accompanied with delayed maturity due to habitat degradation. Sub-par habitat subject mussels to metabolic stress (Layzer, Gordon, & Anderson, 1993) and induce delayed maturity (Bauer, 1983; Way, Miller, & Payne, 1989) which decreased fecundity by 97% (Layzer et al., 1993; Vaughn & Taylor, 1999). Low quality habitat patches with erratic thermal and hydrologic regimes affect the survival of juvenile and adult mussels (D. L. Strayer et al., 2004; Vaughn & Taylor, 1999). Habitat fragmentation was modeled by reducing the patch size and reducing the dispersal rate between patches. This reduction in habitat area and increase in patch isolation had a negative effect on the persistence of Carolina Heelsplitter. Both population systems (N_0=1008 and N=60) reduced the probability of population persistence over the next 50 years. Because all the vital rates were equal among the reference model and the habitat fragmentation model for both population systems, changes in mean abundance and metapopulation occupancy over 50 years can be attributed to changes in landscape structure, especially the distribution and abundance of individual patches.

Impoundments have driven several mussel and freshwater snail species to local extinctions (Layzer et al., 1993; Lydeard & Mayden, 1995; Vaughn & Taylor, 1999). Loss of suitable mussel habitat may occur due to secondary effects of impoundments such as due to cold-hypolimnetic dam discharges, low levels of dissolved oxygen caused by low flow, high biological oxygen demand, isolation of local populations due to barriers present, high levels of copper and ammonia in the water column, drying of downstream stream reaches, excessive siltation and sedimentation and loss of riparian vegetation which destabilizes the stream banks. (Gangloff, Hartfield, Werneke, & Feminella, 2011; Vaughn & Taylor, 1999; Watters, 1999). A threat analysis conducted by Alderman (1998) in an adjacent Stevens creek watershed identified the threats to the Carolina heelsplitter metapopulation which are relevant to the Turkey Creek watershed due to proximity of location. The major threats were water pollution due to municipal runoffs, road and bridge development, channelization, dredging and impoundments. These perturbations occur at the landscape level and mussels particularly the endangered Carolina heelsplitter do not have the opportunity to escape them through long distance dispersal as the identified specific host fish belonging to families Cyprinidae and Centrarchidae can only disperse a maximum distance of 500 meters (Eads et al., 2010).

The results of this study indicate that the decrease in the Carolina heelsplitter metapopulation viability can be linked primarily to the effects of habitat degradation.

Hence the management practices should focus on improving the habitat quality rather than improving the habitat mosaic quantity. This doesn't mean that the conservation strategies should focus on single habitat patch. The management practice will have most success when a network of potentially suitable habitat patches is preserved which allows the species to disperse and cope with local environmental stochasticity. Along with augmentation of species, translocation and reintroduction of freshwater mussels has been an important conservation practice in some restored stream reaches (Jones, Neves, & Hallerman, 2012; R. Neves, 2004). Use of propagation techniques as a restoration and conservation strategy has gained leverage in the recent times especially for small populations of endangered freshwater mussel species whose threats have been ameliorated (Jones, Hallerman, & Neves, 2006). A conservation program with sound aqua-cultural propagation of Carolina Heelsplitter through diverse genetic stock, reintroduction of mussel species and host fish species at restored sites such as those within the Turkey creek watershed and monitoring of the habitat by working with local land-owners and local government departments such as the South Carolina Department of Natural Resources (DNR) and Department of Transportation (DOT) could also play a key role in re-establishing viable Carolina Heelsplitter metapopulations with a potential of the species being delisted in the near future.

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Table 4-1: Model parameter estimates used in metapopulation analysis of the Carolina heelsplitter metapopulation in Turkey Creek watershed, Savannah River Basin, SC. (REF= Reference, HF= Habitat fragmentation, HD= Habitat degradation, HF+HD= Combined effect)

Parameter	**Estimates**				**Source**
	Scenario 1 (REF)	**Scenario 2(HF)**	**Scenario 3 (HD)**	**Scenario 4 (HD+HF)**	
Survival in stage matrix	Recruit =0.74 Juvenile=0.37 Adult =0.555	Recruit =0.74 Juvenile=0.37 Adult =0.555	Recruit =0.74 Juvenile=0.37 Adult =0.555	Recruit =0.74 Juvenile=0.37 Adult =0.555	(Haag & Leann Staton, 2003; Haag, 2012b; R. F. Villella, Smith, & Lemarié, 2004)
Fecundity in stage matrix	Recruit =0.0 Juvenile=0.0 Adult =1.025	Recruit =0.0 Juvenile=0.0 Adult =1.025	Recruit =0.0 Juvenile=0.0 Adult =1.025	Recruit =0.0 Juvenile=0.0 Adult =1.025	
Relative survival for all life stages	1.0	1.0	Varies between 1.0 (least affected) to 0.5 (most affected)	Varies between 1.0 (least affected) to 0.5 (most affected)	
Relative Fecundity	1.0	Populations closet to barriers have RF= 0.8	Varies between 1.0 (least affected) to 0.5 (most affected)	Varies between 1.0 (least affected) to 0.5 (most affected)	
Population growth rate	$\lambda = 1.006$	Varies between λ = 1.006 and 0.9562 for some populations	Varies between λ = 1.006, 0.8004 and 0.5003 for some populations	Varies between λ = 1.006, 0.8004 and 0.5003 for some populations	(Haag, 2012b)
Initial Abundance	R, J, A (N_{1000}) = 4,6,4 R, J, A (N_{60}) = 2,2,2 or 1,2,1 or 1,1,1	R, J, A (N_{1000}) = 4,6,4 R, J, A (N_{60}) = 2,2,2 or 1,2,1 or 1,1,1	R, J, A (N_{1000}) = 4,6,4 R, J, A (N_{60}) = 2,2,2 or 1,2,1 or 1,1,1	R, J, A (N_{1000}) = 4,6,4 R, J, A (N_{60}) = 2,2,2 or 1,2,1 or 1,1,1	

Carrying Capacities (K)	1000 for all habitat patches	500 (low quality habitat patches) 1000 (rest of the patches)	500 (low quality habitat patches) 1000 (rest of the patches)	500 (low quality habitat patches) 1000 (rest of the patches)	
Local populations	$(N_{1008}) = 72$ $(N_{60}) = 15$	$(N_{1008}) = 72$ $(N_{60}) = 15$	$(N_{1008}) = 72$ $(N_{60}) = 15$	$(N_{1008}) = 72$ $(N_{60}) = 15$	(Alderman, 1998; NatureServe, 2011; USFWS, 2012)
Correlation	50% for populations in same stream 25% for populations amongst streams	50% for populations in same stream 25% for populations amongst streams	50% for populations in same stream 25% for populations amongst streams	50% for populations in same stream 25% for populations amongst streams	
Dispersal	a= 1.0 b= 300m D_{max}=3000m Relative Dispersal= 1.0	a= 0.5 b= 300m D_{max}=3000m Relative Dispersal= 0.8	a= 1.0 b= 300m D_{max}=3000m Relative Dispersal= 1.0	a= 0.3 b= 300m D_{max}=3000m Relative Dispersal= 0.5	(Eads et al., 2010; Schwalb et al., 2011)

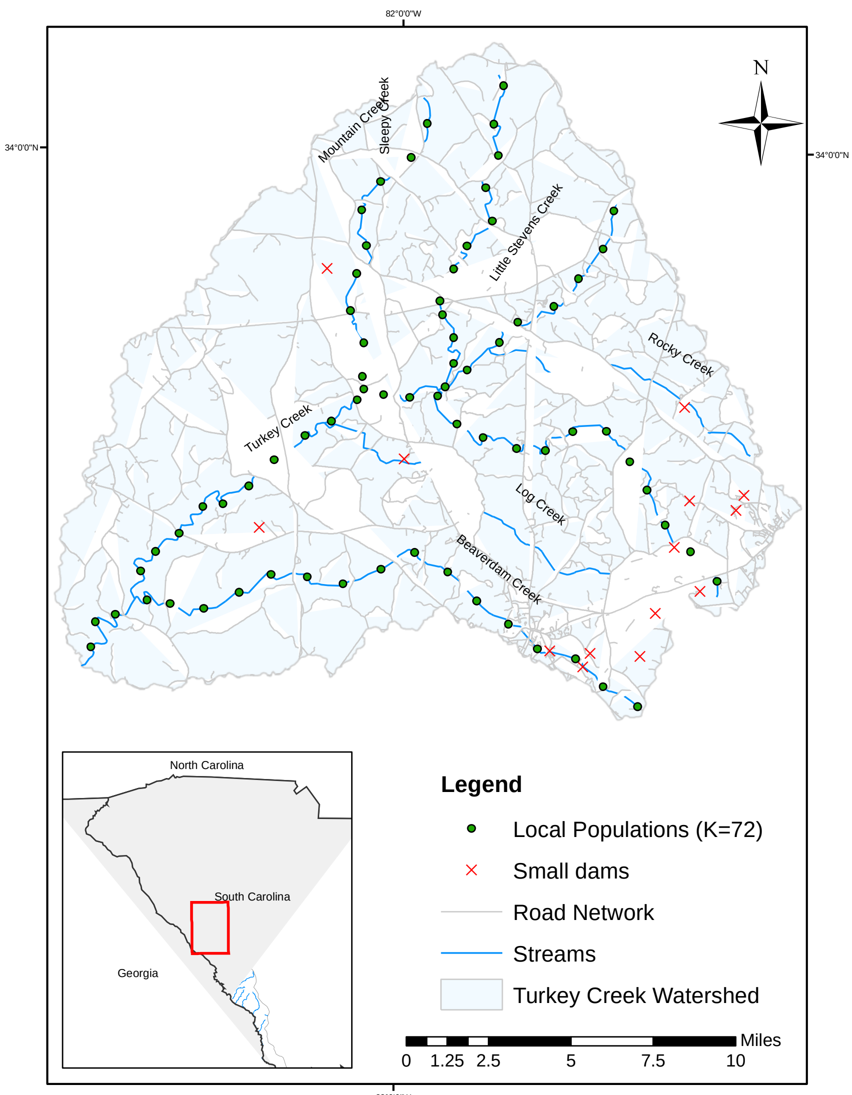
Table 4-2: Sensitivity of the Carolina heelsplitter N_0 metapopulation results to parameters given in form of probability of 90% Decline (below 100 individuals after 50 years). Each parameter is varied individually while all other are held constant.

Parameter	% change		Probability of 90% Decline (Absolute[16] and Percent[17])			
		Effect[18]	REF	HF	HD	HD + HF
Baseline Model	λ=1.006		< 0.01	< 0.01	0.398	0.4340
Stage Matrix means	+10%, λ=1.1006	+	< 0.01 100%	< 0.01 100%	< 0.01 100%	< 0.01 100%
	-10%, λ=0.9005	-	0.99 9900%	0.99 9900%	0.99 250%	0.99 230%
Stage Matrix Std. deviations	+10%	+	< 0.01 100%	< 0.01 100%	0.4030 102%	0.4060 94%
	-10%	-	< 0.01 100%	< 0.01 100%	0.4010 101%	0.4030 93%
Initial Abundance	+10%	+	< 0.01 100%	< 0.01 100%	0.4080 103%	0.4060 94%
	-10%	-	< 0.01 100%	< 0.01 100%	0.4310 108%	0.4360 101%
Carrying capacities (K)	+10%	-	< 0.01 100%	< 0.01 100%	0.4290 108%	0.4300 99%
	-10%	-	< 0.01 100%	< 0.01 100%	0.4150 104%	0.4210 97%
Dispersal Rates	+50%	-	< 0.01 100%	< 0.01 100%	0.4180 105%	0.4470 103%
	-50%	+	< 0.01 100%	< 0.01 100%	0.4130 104%	0.4160 96%

[16] The absolute estimate of the parameter
[17] The percentage of the result with the initial value of the parameter
[18] The effect of increasing the parameter on metapopulation viability. Indicates whether the parameter increased (+) or decreased (-) the persistence of the metapopulation.

Figure 4-1**:** Adult Carolina heelsplitter found at Mountain Creek, South Carolina.

Figure 4-2: Patch structure of the Carolina Heelsplitter metapopulation in Turkey Creek watershed, South Carolina. Road density is represented by grey lines and location of small dams[19] within the watershed are represented by red crosses and the black outline is the border of the study area.



[19] Several small mill and pond dams are on ephemeral streams that feed into the streams and creeks with the Turkey creek watershed.

Figure 4-3: Life-cycle diagram for the Carolina Heelsplitter. Stages include Recruits, Juveniles and Adults. Grey dashed arrow represents fecundity and black bold arrows represent survival (transitions to next stage or stay-in-stage transitions).

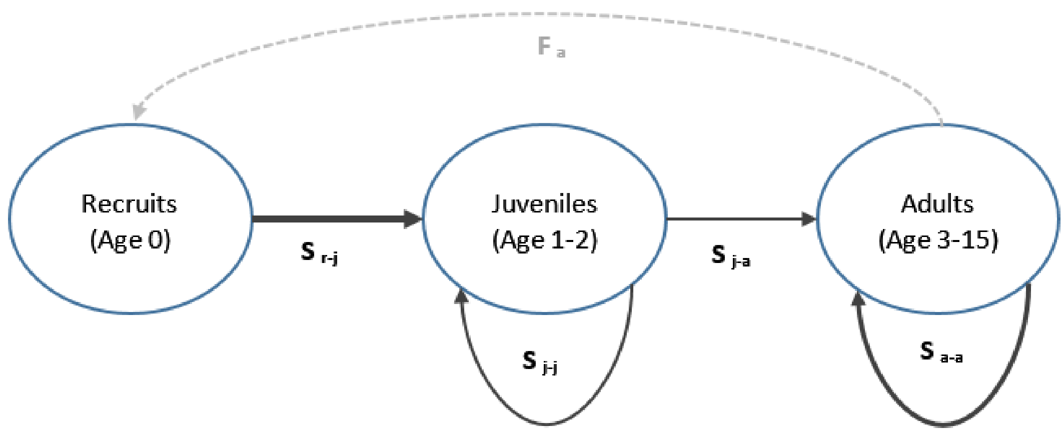


Figure 4-4: Proportion of dispersing Carolina heelsplitter recruits as a function of distance (in meters). *The curve is a function of* $\mathrm{M} = 1 * \exp -\mathrm{x}/300$. Data from (Schwalb et al., 2011).

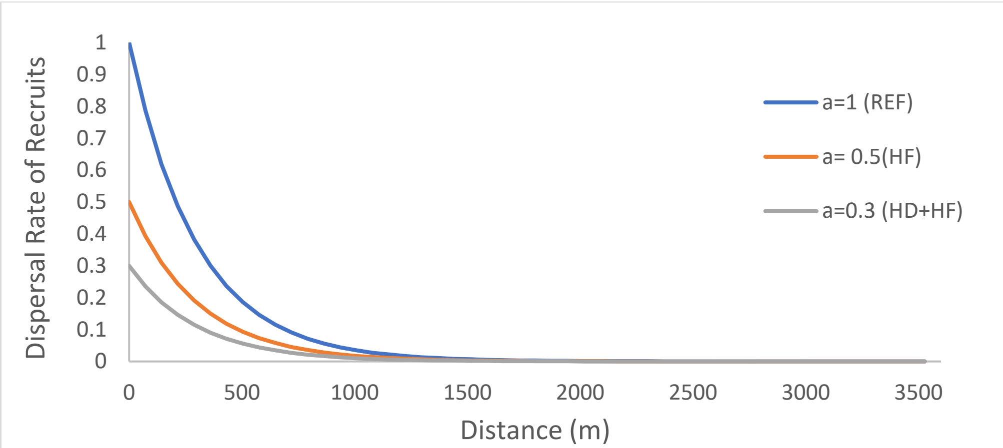
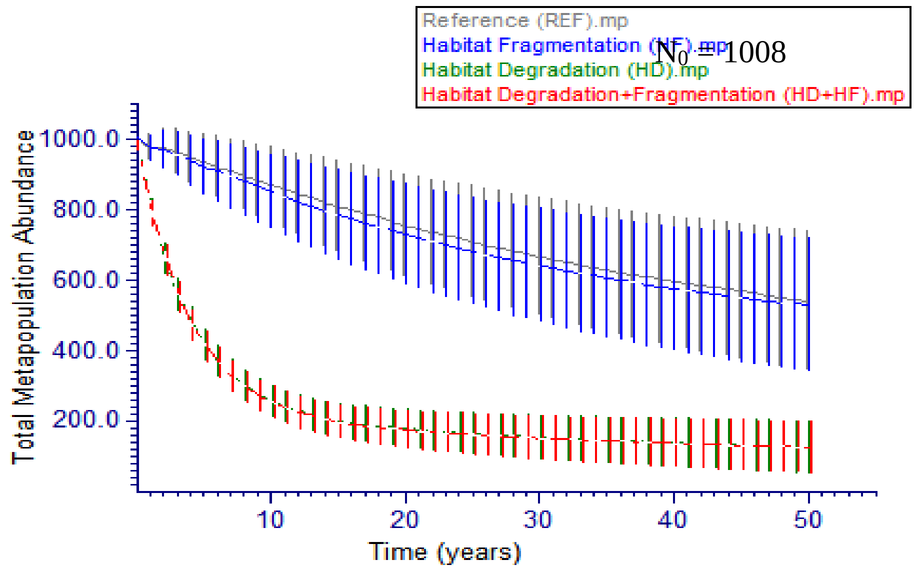


Figure 4-5: Change in mean population size of Carolina heelsplitter metapopulation, under the influence of the four scenarios. a) N_0= 1008 b) N=60

a)



b)

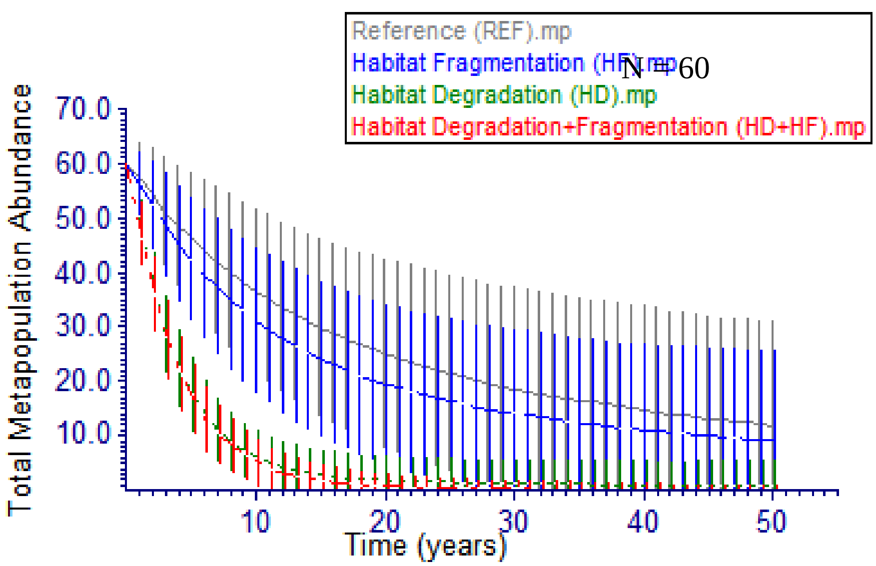
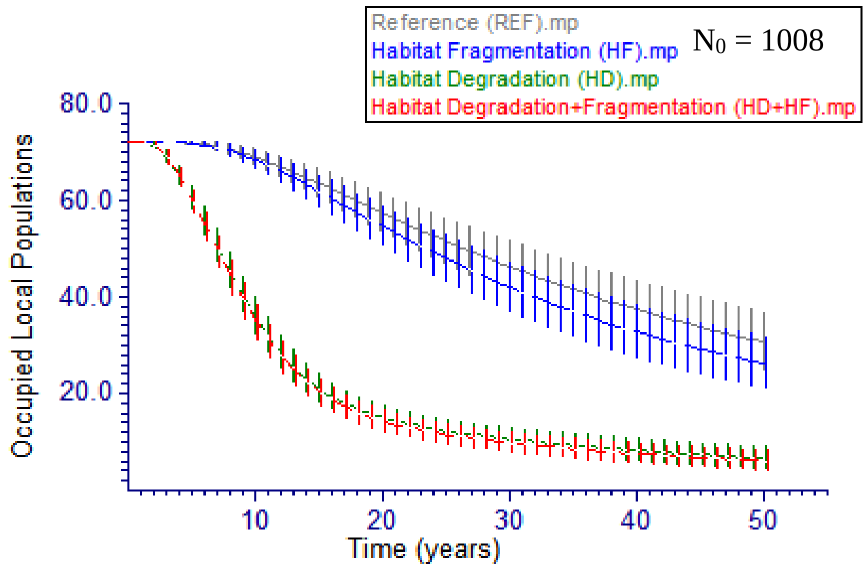


Figure 4-6: Patch Occupancy of local populations of Carolina Heelsplitter through 50 years. a) N_0= 1008 b) N=60

a)



b)

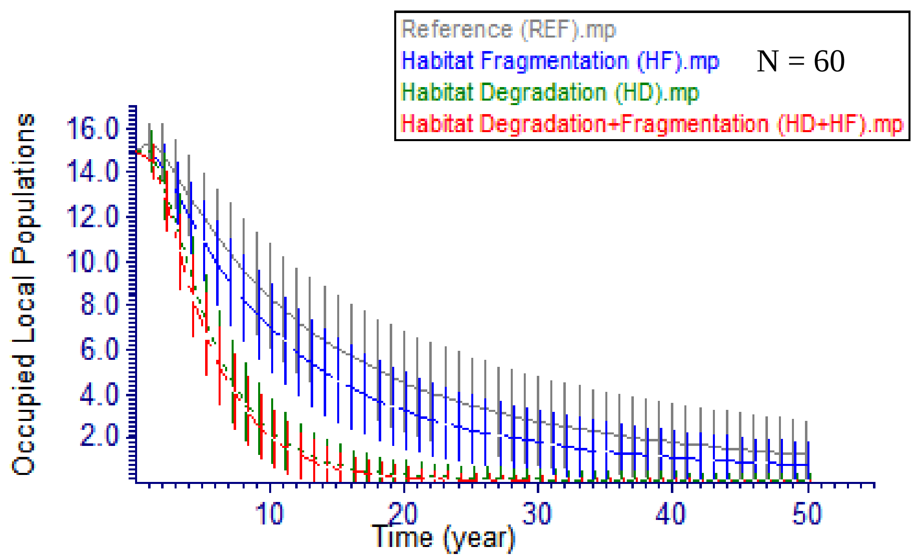
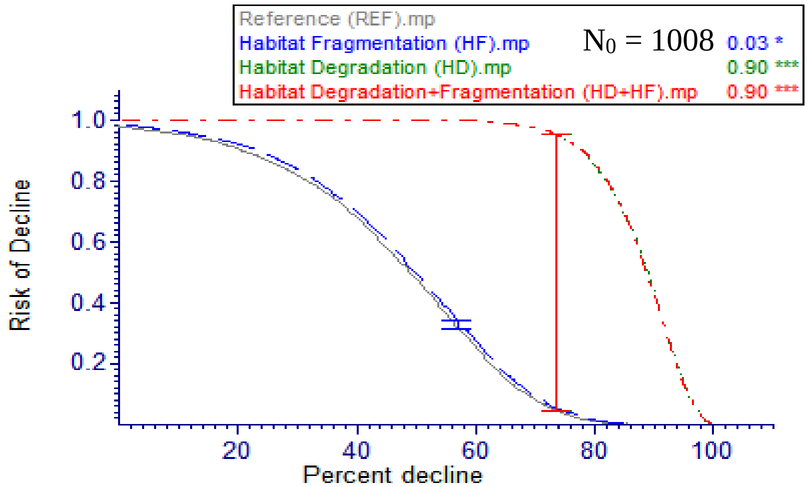


Figure 4-7: Risk of the Carolina heelsplitter Metapopulation decline as a function of the amount of decline or magnitude predicted by the four scenarios; reference, effects of habitat degradation, habitat fragmentation and combined effects of both. a) N_0= 1008 b) N=60

a)



b)

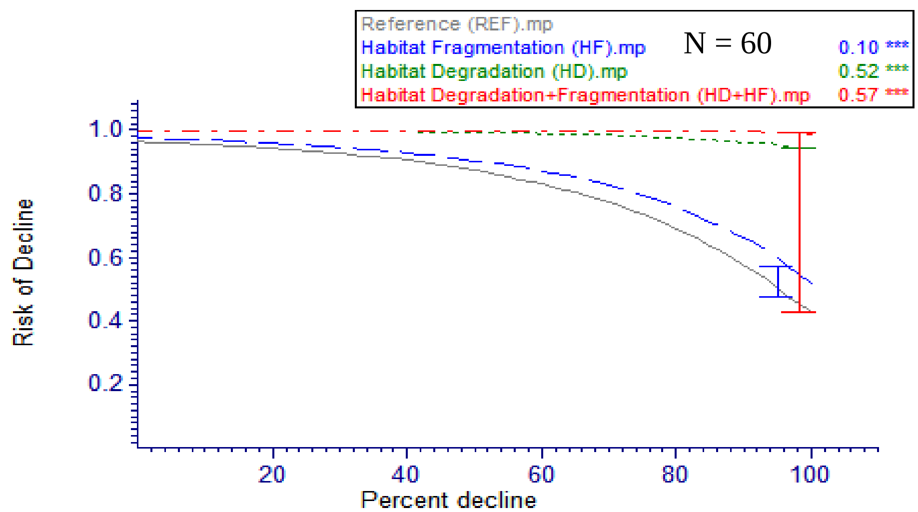
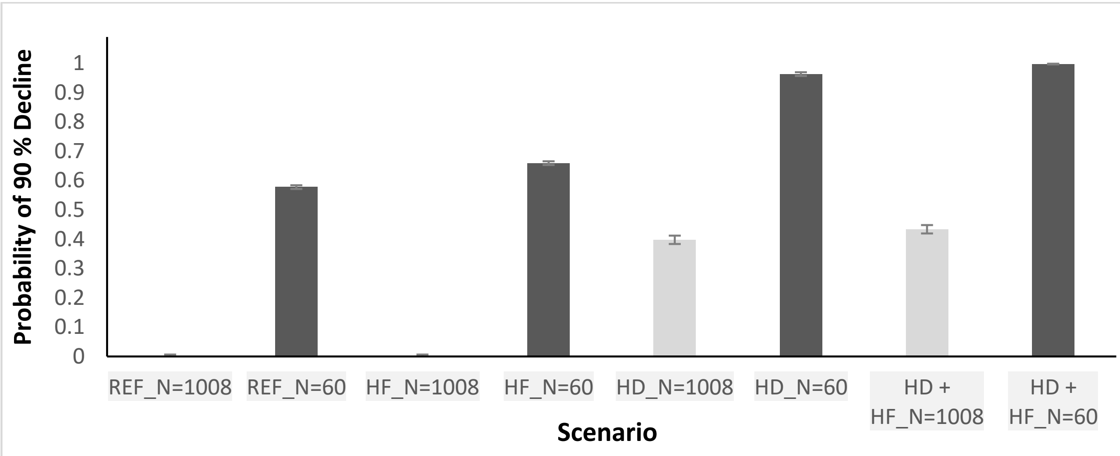


Figure 4-8: Probability of observing a 90% decline (+ standard error) in Carolina heelsplitter metapopulation in 50 years with four scenarios and for two populations, N_0=1000 (in light grey) and N=60 (in dark grey).



CHAPTER FIVE

CONCLUSIONS

SIGNIFICANT FINDINGS

This dissertation comprises of multiple approaches to quantify the impact of energy production on freshwater mussel ecology and provides insights into the species' response to habitat loss in form of habitat degradation and fragmentation.

In Chapter Two, I explored the temporal connection between electricity generation and water use at three spatial scales – National, Regional and Local. The results from this chapter suggested that with increasing demand for electricity irrespective of the policies in place and the choice of energy mix, there will be an increase in water use particularly water consumption with water withdrawals varying largely with the region and the choice of energy mix and cooling technologies.

In Chapter Three, I statistically analyzed the influence of local and landscape driven factors on the distribution and occupancy of freshwater mussels in the Savannah Basin which exhibits water-stress owing to water appropriation by electricity generation facilities. The results support the claim that different freshwater mussel species respond to a variety of local and landscape factors having diverse management implications. The presence of impoundments has a strong negative association with the occurrence of highly-fragmented mussel populations especially the high priority species such as *Lasmigona decorata* and *Alasmidonta varicosa*.

Finally, in Chapter Four, I developed a metapopulation model to predict the population viability of endangered Carolina heelsplitter (*Lasmigona decorata*) under the scenarios of habitat degradation, habitat fragmentation and a combined effect of both. Habitat loss primarily from habitat degradation has a more pronounced negative effect on the Carolina heelsplitter metapopulation persistence than habitat fragmentation which played a significant role in metapopulation decline only when the initial population size was low.

MANAGEMENT RECOMMENDATIONS

Global warming is expected to increase the frequency of unpredictable climate related phenomenon such as floods, droughts, hurricanes and sea-level rise in the United States. These catastrophes make energy production vulnerable due to their significant demand on water resources. The Clean Power Plan introducted during the Obama administration aimed at reducing dependence on fossil fuels particularly coal, by regulating emissions from new power plants, making it challenging to build new thermal-power plants hence encouraging energy efficiency and subsidizing clean renewable energy (Obama, 2017) all of which would eventually contribute to sustainable water use by the energy-sector. However, in lieu of the recent proposal to repel the Clean Power Plan (Friedman & Plumer, 2017, October 9), the impact on the energy sector and the subsequent water security of the United States will be under scrutiny. How the fate of the Clean Power Plan plays out will have a profound effect on the environment and our natural resources.

The water-energy nexus is governed on multiple levels. In the United States, energy is considered a national security issue while water is managed mostly by regional or state agencies (Charbit, 2011). Policies and regulations that regulate water management at local and regional level should work in synergy with the energy policies implemented at the national level. The research conducted by regional agencies with respect to water supply, energy generation and health of aquatic ecosystems can be implemented in policies at national level to regulate the environmental impacts of energy production. A few policy recommendations that might aid in reducing energy sector's impacts on water resources would be to enforce stricter regulations on water quality and $CO_2/NO_x/SO_x$ emission standards and to encourage energy efficiency and grid modernization. At regional and local scale, before the licensing and relincensing, power plant owners and leasing authorites ought to take into consideration the environmental risks associated with current water use in the basin and the growing challenge of water availability for the new or existing plants (Carrillo & Frei, 2009). Depending on the power plants, measures such fish nets and correct design and type of fish screens may be implemented to prevent entrainment and impingement of fish and macroinvertebrates. However, caution must be maintained as the use of fish screens may benefit only if routine long-term maintenance program is part of the installation project (Schilt, 2007). In case of hydropower plants, use of fishways (fish ladders/lifts/lorries) and fish handlers (capture and hauling) for upstream passage of adult fishes and turbine intake screens to divert juveniles from turbine intakes into bypass facilities may be of benefit (Schilt, 2007). Futhermore, power plants can consider adopting cooling technologies that are more water-conserving such as dry or hybrid cooling.

The conservation and management plans need to account for the multiple stressors that are responsible for the decline of freshwater mussels (Alderman, 1998; Nobles & Zhang, 2011). The Savannah River basin may benefit most from an integrated management approach involving protecting and restoring the riparian and aquatic ecosystems, mandatory impact assessment of anthropogenic disturbances, sustainable agricultural and industrial activities involving energy production, and enforcing water quality and environmental flows standards. The results of this study identifies the need to fill the existing knowledge gaps by surveying small order streams in the piedmont region of South Carolina, monitoring long term population trends and assessing conservation status of threatened freshwater mussel species. Chapters three and four of this dissertation provide foundation to construct models that can predict relationships between habitat/landscape factors and distribution of the freshwater mussels as well as estimate the impacts of threats on freshwater mussel metapopulation viabilities. These models can serve as a planning tool informing management decisions such as prioritization of habitat protection and restoration over removal of dispersal barriers. These models may find applicability as a mitigation tools to be used by state and federal agencies for conservation planning to evaluate the risk of a metapopulation extinction given the increased water use scenarios in the basin or predict metapopulation persistence in case of a reintroduction attempt by relocating mussels to suitable habitats in stream reaches that are currently not occupied.

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